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Late Cretaceous-early Tertiary echinoids from northern Spain: implications for the Cretaceous-Tertiary extinction event

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CONTENTS

Synopsis. The Maastrichtian and Palaeocene echinoid faunas are described from Santander, Province of Cantabria, the Basque region of Spain and France, and the region around Irurtzun, Province of Navarra. These deposits range from shallow shelf carbonates to upper continental slope clastics. A total of 58 species are described, 40 from the Maastrichtian, nine from the Danian and nine from the Thanetian. Echinoid extinction is estimated to be around 40% in shallow water settings, but may have been more intense in deeper settings. Extinction levels are comparable with the other well-studied western European faunas of the Danish basin and the Limburg region. A striking shift in the geographic ranges of taxa took place between the end of the Cretaceous and the Palaeocene. Taxa migrated both from the Danish basin southwards and from the Tethyan region northwards at this time.

The first fossil representative of the Recent deep-sea family Aeropsidae is described from the early Thanetian of Navarra. New taxa described here include the genus *Sphenaster* and the species *Tylocidaris trempinus, Camerogalerus cantabrius, Adelopneustes ernsti, Stegaster palaeocenicus, Ovulaster reticulatus* and *Sphenaster larumbensis.*

INTRODUCTION

The end of the Cretaceous saw the extinction of many marine invertebrates, but precisely what events brought about this extinction, and over how short a time interval these events took place remain the subject of heated debate. Most research so far has been directed towards documenting the synchroneity and duration of extinctions, through microstratigraphical sampling in 'complete' boundary sections (e.g. Marshall & Ward, 1996, MacLeod, 1998). Much less emphasis has been given to the ecological and geographical pattern of extinction at this time, with the notable exception of Jablonski & Raup (1994) and Smith & Jeffery (in press). Understanding what, if any, environmental pattern there is to survivorship

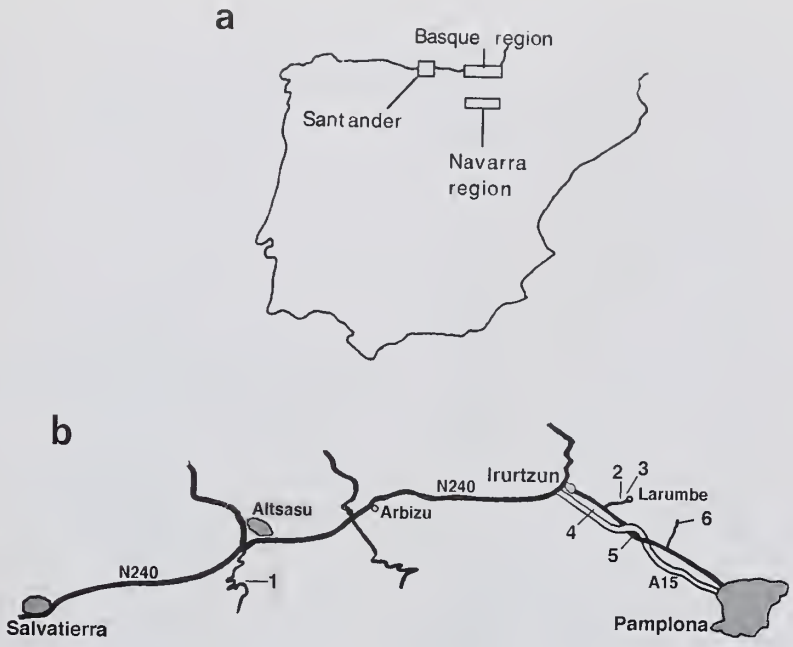


Fig. 1 Location maps. **a,** The three main areas in Spain and southern France from which the echinoid faunas are described. **b,** The location of the main echinoid-bearing horizons in the Irurtzun region, Navarra, studied in this paper. 1 = Olazagutia Pass; 2 = Casas de Oraien; 3 = Larumbe; 4 = Sarasate; 5 = Erice; 6 = Aristregui.

should help shed light on the immediate causes that led to the end Cretaceous extinctions.

We have been studying the echinoid faunas on either side of the Cretaceous – Tertiary boundary from three regions in Northern Spain. These faunas come from the open shelf sandy carbonate succession to the West of Santander, the continental slope deposits of the Basque region (Sopelana to Bidart), and the carbonate platform to intraplatform basinal facies around Irurtzun in the Province of Navarra (Fig. 1a). New collections from the Santander region (Gallemí, Jeffery & Smith), Basque region (Peter Ward) and Navarra region (Ernst, Gallemí, Jeffery & Smith) have been made, and the taxonomy updated and standardized. Using this new data we compare levels of extinction in the three faunas to see if there is any environmental signal. We also compare the level of extinction in northern Spain with that recorded from other European regions, specifically with Limburg and the Danish basin, to discover whether there is a latitudinal bias to extinction at this time. It has been shown that foraminifera suffered less intense extinction at higher palaeolatitudes (MacLeod & Keller, 1994, MacLeod, 1995) whereas no such pattern was evident for molluscs (Jablonski & Raup, 1994).

GEOLOGICAL SETTING

The late Cretaceous is represented by a wide range of facies and palaeoenvironments in the Basco-Cantabrian basin of northern Spain. By middle Campanian times this region formed a single flysch trough with lateral slope deposits, bordered by narrow shelf platforms. The southern margin of the evolving Biscay ocean developed as a series of pull-apart basins (Wiedman *et al.*, 1983) which became progressively more strongly affected by strike-slip tectonics to the east. Shallow-water carbonate facies developed across this narrow shelf, with black shale facies forming in local basins. The Biscay trough extended approximately east-west along the line now formed by the Pyrenees. This oceanic arm, which is estimated to have had a palaeodepth of approximately 1,500 m (Delacotte, 1982), separated the shallow marine deposits of the Navarra-Cantabria platform to the south from the corresponding shallow shelf deposits of the South Aquitaine platform to the north-east.

There is a strong sea-level signature recognizable in the deposits of this region. Maastrichtian deposition falls within a single sea-level cycle (Wilmsen *et al.*, 1996). A major facies change occurs more or less coincident with the K-T boundary, brought about by rapid sea-level rise (Haq *et al.*, 1987, Keller *et al.*, 1993). During the Danian sea-level fell gradually, but began to rise once more in the late Thanetian. Climate towards the end of the Cretaceous was deteriorating (Barrera, 1994).

DETAILS OF SECTIONS

The Santander region

In the immediate vicinity of Santander, from Cabo Mayor westwards, Maastrichtian–Palaeocene sediments are exposed along the coastal cliffs (Fig. 2). The stratigraphy of this section has been studied in detail by Heredia *et al.* (1990) as part of the geological mapping of Cantabria. Here the Upper Campanian to Maastrichtian beds belong to the Cabo de Lata Formation (García-Mondéjar & Pujalte, 1982). The Maastrichtian part of the succession falls within a single sea-level cycle referred to as Megasequence 5 by Wilmsen *et al.* (1996). The basal beds comprise cross-bedded calcarenites with many hardgrounds and temporary hiatuses in sedimentation, and were deposited under falling sea-level. The presence of occasional tempestites suggests deposition within storm wave-base.

Fig. 2. Map showing the location of the main echinoid-bearing horizons in the Santander region, Cantabria, studied in this paper.

There then follows a thick succession of bedded sandy limestones, with thin calcarenitic limestones, and evidence of surge channels and tempestites (Wilmsen *et al.*, 1996), indicative of deposition within normal wave-base. This part of the succession was deposited under rising sea-level. There are a few thin conglomerates and shell-rich calcarenites which probably represent storm debris flows from near-shore habitats.

The upper beds become unfossiliferous, and return to a series of thinner bedded calcarenites and sandy limestones with abundant hiatuses and hardgrounds; they are dolomitized and were presumably emergent. Consequently, the boundary between the Maastrichtian and Palaeocene cannot be determined on faunal grounds. The dolomites are microcrystalline, or occasionally pseudo-oolithic, with sparse gastropods and ostracods seen in cross-section, and are succeeded by a thin succession of calcarenites full of hardgrounds and sedimentary hiatuses. Above, there are thicker-bedded calcarenites with abundant asteroid ossicles, sandy in some levels, and with abundant Rhodoficiae algae and Microcodium at the base. These dolomites and calcarenites together form the San Juan Formation, and have been attributed to the Danian and Montian. The succession is capped by a very thin series of calcarenites with glauconite, the Sancibrián Formation, which has a Thanetian microfauna (Heredia *et al.*, 1990).

In terms of depositional environment, the Cabo de Lata Formation represents relatively shallow inner platform clastics deposited within fair-weather wavebase (Heredia *et al.*, 1990). The presence of echinoids in these beds was first noted by Jiménez de Cisneros (1910) and Mengaud (1910), who correctly attributed these beds to the Maastrichtian. Jiménez de Cisneros (1912) listed the following echinoid species as coming from Santander: *Echinoconus conicus* Breynius [=*Galerites albogalerus* Klein], *Echinocorys vulgaris* Breynius, *E. conicus* Breynius, *Hemipneustes pyrenaicus* Hébert, *Hemiaster prunella* Desor and *Cidaris* cf. *C. subvesiculosa* d'Orbigny. Later, Lambert (1920–22) identified five echinoids from the Maastrichtian of this area; *Tylocidaris ramondi* Leymerie, *Conulus gigas* Cotteau, *Clypeolampas leskei* Goldfuss, *Hemipneustes pyrenaicus* Hébert and *Echinocorys tercensis* Lambert. Wilmsen *et al.* (1996) noted the presence of several echinoid events and listed a number of genera and species.

The San Juan Formation is interpreted as being deposited in a shallow, restricted internal platform setting, which becomes progressively less restricted upwards into the Sancibrián Formation.

Echinoids have been collected from 9 levels at ten localities along the cliff section west of Santander (Figs 2, 3).

The Basque region

Only deep-water Maastrichtian–Palaeocene facies are represented in the Basque region. During the early Maastrichtian continental slope turbidites were deposited. However, near the end of the early Maastrichtian there was a marked reduction in siliciclastic input, probably marking the world-wide late Maastrichtian regression. Following the K-T boundary there was an even more dramatic reduction in siliciclastic input to the basin, resulting in the deposition of pink coccolith limestones (commonly resedimented) during the Danian (Ward & Kennedy, 1993). Hiatuses and non-depositional surfaces are common in these Danian beds reflecting a major rise in sea-level.

From their study of coastal stratigraphical sections of the Zumaya-Algorri Formation at Sopelana, Zumaia, Hendaye and Bidart, Ward & Kennedy (1993) recognised five Maastrichtian units, referred to as Members I-V. Echinoids are found throughout the section 'but never in great abundance, and only rarely in bedding plane concentrations' (Ward & Kennedy, 1993). They are most common in Members IV and V. We have plotted the stratigraphic occurrence of echinoids from these localities onto a single standard section, Ward & Kennedy's (1993) Zumaia lithological section (Fig. 4).

The echinoid fauna from this region has not been studied since the

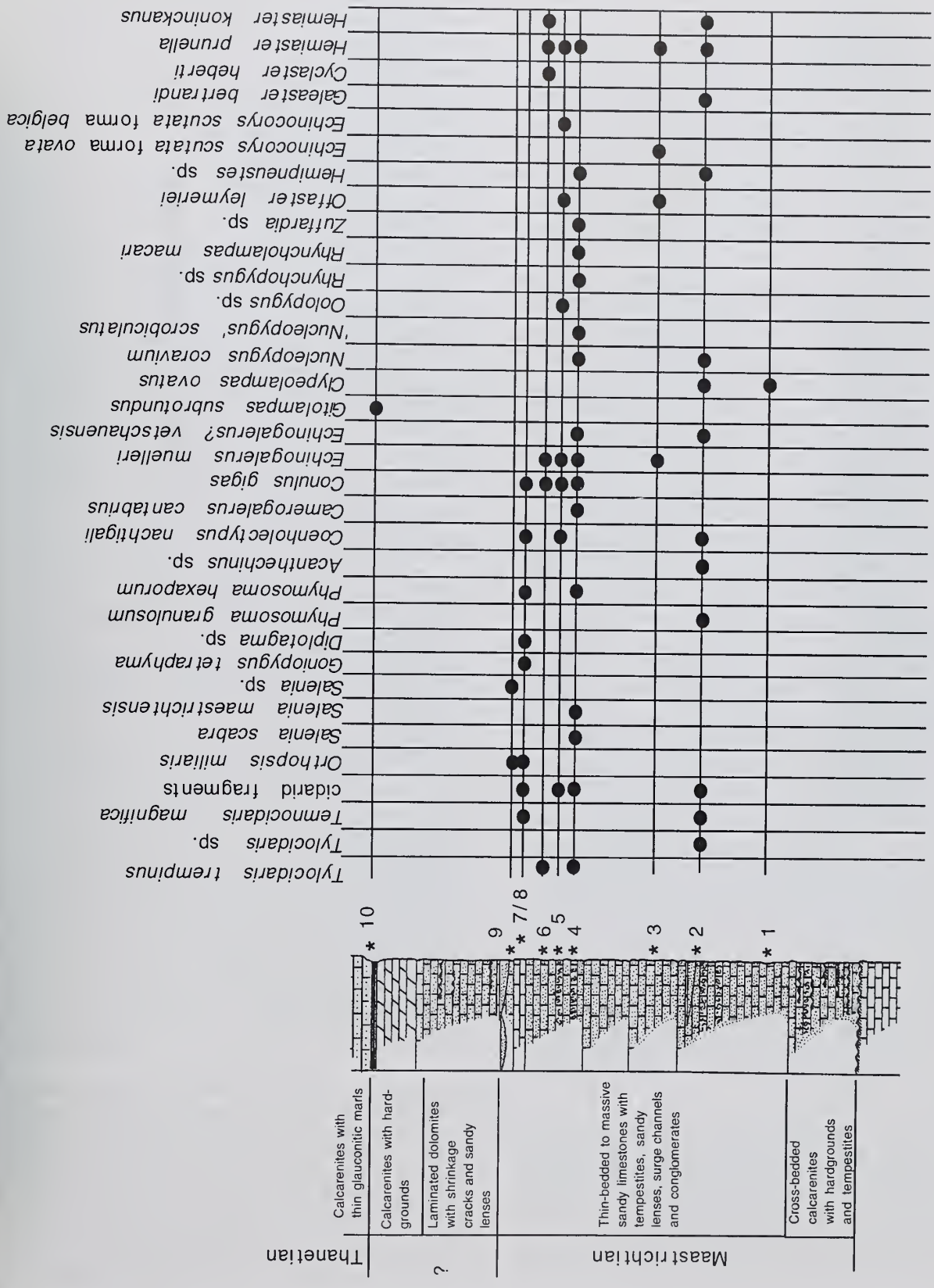


Fig. 3. Stratigraphic section of the Maastrichtian section to the West of Cabo Major, near Santander, Cantabria, showing the distribution of echinoids.

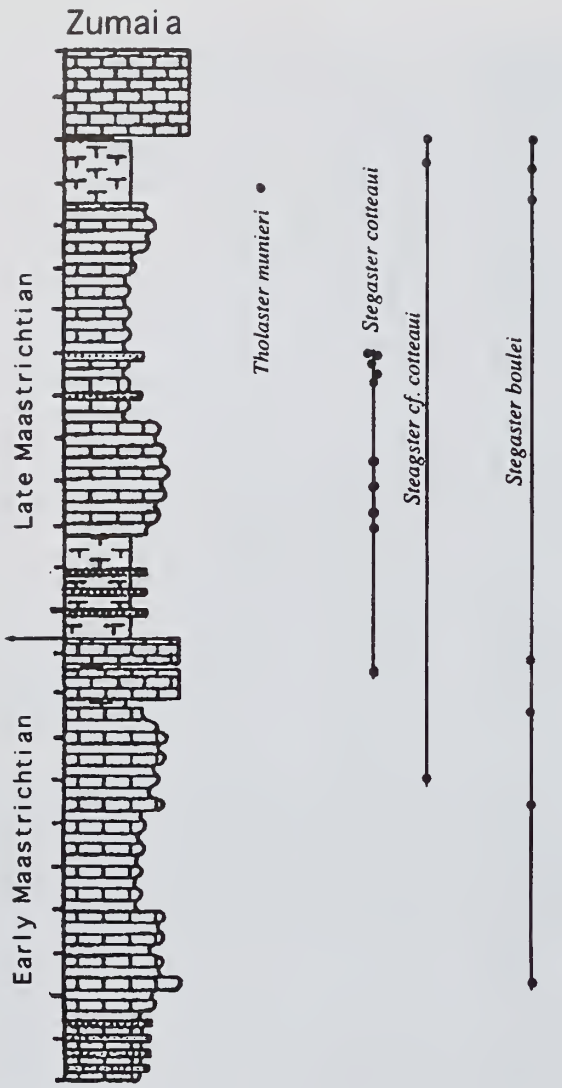


Fig. 4 Composite stratigraphic section of the Maastrichtian of the Basque region from Zumaia, Gipuzkoa, Spain to Bidart, Pyrenées-Atlantique, France (from Ward & Kennedy 1993) showing the distribution of echinoids.

pioneering work of Seunes (1888a, 1888b and 1889). He reported the occurrence of *Cidaris beaugeyi* Seunes, *Jeronia pyrenaica* Seunes, *Coraster beneharnicus* Seunes, *Echinocorys douvillei* Seunes, *Stegaster heberti* Seunes, *S. bouillei* Cotteau, *Gibbaster munieri* Seunes [=*Tholaster munieri* (Seunes)] and *Galeaster bertrandi* Seunes from the vicinity of Bidart.

The Navarra region

This has the most complicated geology of the three regions, being strongly affected by strike-slip faulting. Maastrichtian deposits are represented by two facies: shelf platform carbonates (studied at Olazagutia Pass) and shelf basinal mudrocks (studied at Larumbe and Sarasate) (Fig. 1b). Table 1 lists the echinoids collected from this region. The overlying Danian and early Thanetian consist of a sequence of coccolith limestones that in places includes reworked pebble beds.

Table 1 Echinoids from the Navarra district (see Fig. 1b for map of area).

LOCALITY 1. Maastrichtian, carbonate platform facies; Olazagutia Pass.

Tylocidaris (Sardocidaris) ramondi (Leymerie)
cidaroid plates indet.
Salenia (Pleurosalenia) maastrichtensis Schlüter
Conulus gigas (Cotteau)
Echinogalerus muelleri (Schlüter)
Nucleopygus scrobiculatus (Goldfuss)
Offaster leymeriei Cotteau
Hemipneustes pyrenaicus Hébert
Hemipneustes striatoradiatus (Leske)
Hemiaster koninckanus d'Orbigny
Hemiaster prunella (Lamarck)
Cyclaster sp.

LOCALITY 2. Late Thanetian, Casas de Oraien.

Gauthieria pseudomagnifica (Cotteau)
Adelopneustes ernsti sp. nov.
Cardiaster sp.
Isaster aquitanicus (de Grateloup)
Echinocorys scutata forma *cotteaui* Lambert
Micraster tercensis Cotteau
Hemiaster stella (Morton)
Linthia sp. Cotteau

LOCALITY 3. Danian-early Thanetian at Larumbe.

Coraster vilanovae Cotteau
Coraster beneharnicus Seunes
Sphenaster larumba sp. nov.
Jeronia pyrenaica Seunes
Echinocorys sp.

LOCALITY 4. Maastrichtian; basinal facies.

Motorway cutting at Sarasate, just South-East of Irurzun.
Stegaster bouillei (Cotteau)
Stegaster altus Seunes
Echinocorys scutata forma *ovata* Leske
Ovulaster reticulatus sp. nov.
Pseudoffaster caucasicus (Dru)
Cyclaster sp.
Danian near summit of hill at Sarasate
Cyclaster aturicus (Seunes)
Cyclaster gindrei (Seunes)
Coraster beneharnicus Seunes

LOCALITY 5. Danian of Erice.

Coraster vilanovae Cotteau
Coraster beneharnicus Seunes
Cidaroid spines
Echinocorys scuata forma *pyrenaica* Seunes
Cyclaster grindrei (Seunes)

LOCALITY 6. Late Danian at Aristregui.

Stegaster paleocenicus sp. nov.
Jeronia pyrenaica Seunes
Coraster vilanovae Cotteau
Echinocorys scutata Leske

Olazagutia Pass. The carbonate platform succession was studied at Olazagutia Pass (Fig. 1b), the type locality of the Puerto de Olazagutía Formation (Amiot, 1982), along the road leading from Olazti to the Urbasa Range. The units that lie at the top of the Olazagutía Formation yield the richest and most varied fauna. These beds were deposited in an external platform setting (Amiot, 1982).

Here the Maastrichtian succession commences with a massive bedded limestone (Fig. 5). This is succeeded by a series of thinner sandy limestones, calcareous sandstones and marls which are richly fossiliferous. A thick sandy marl with a rich bryozoan fauna at the

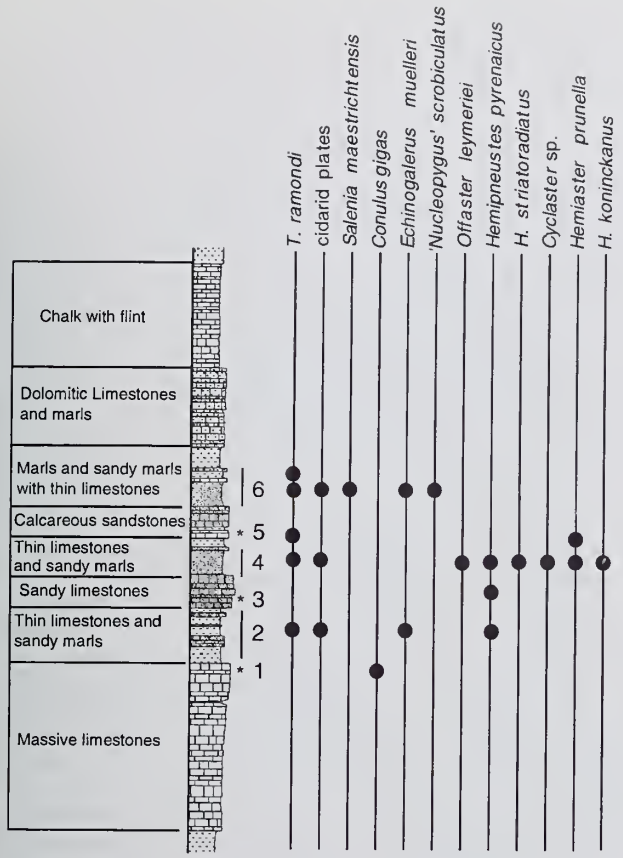


Fig. 5 Stratigraphic section through the Maastrichtian at Olazagutia Pass, Navarra, showing the distribution of echinoids.

top is followed by dolomitized limestones and more massive dolomites. The entire succession apparently represents a shallowing upward cycle, presumably correlatable with the upper part of the Cabo de Lata Formation in Santander.

This locality was first studied by Ruiz de Gaona (1943) who recorded a single echinoid (*Salenia*) from it. A detailed stratigraphic section was published by Amiot (*in* Ciry *et al.*, 1967) and its microfauna studied by Ramírez del Pozo (1971). Ramírez del Pozo recorded the following from this section: *Orbitoides media, Siderolites calcitrapoides, Lepidorbitoides socialis, Globotruncana contusa, Marssonella* cf. *trochus, Nummofallotia cretacea, Omphalocyclus macroporus* and *Racemigumbelina fructicosa*, amongst others, suggestive of a Late Maastrichtian age. A small number of echinoids have previously been reported from this section by Radig (1973).

Erice. A former limestone quarry on the northern side of the motorway A15 in the vicinity of Erice, exposes Cretaceous and Danian sediments. The succession commences with a series of alternating marly limestones and marls containing ammonites and large *Echinocorys*, considered to be Late Campanian in age. There is then a sharp break, probably representing a faulted contact, after which come a succession of deep-water, light-coloured limestones, in part conglomeratic, and locally showing slump fabrics. These are thick to medium-bedded at the base, but more thinly bedded upwards. The lower beds yield a fauna that includes *Coraster vilanovae*, *Cyclaster gindrei* and *Echinocorys scutata* forma *pyrenaica*, that in this area characterizes the upper part of the Danian.

Sarasate. Alternating grey to blue (sometimes slumped) marly limestones and dark shales crop out immediately to the north of motorway A15 at the foot of Sarasate hill, south-west of the town of Irurtzun. Their macrofauna is limited to inoceramids, echinoids, less common brachiopods and rare ammonites, all of them attributed to the Maastrichtian. They were deposited in a shelf basin or shelf margin setting. Echinoids from here include *Stegaster altus* Seunes, *S. bouillei* Cotteau and *Echinocorys scutata* forma *ovata* Leske.

Higher up the hill (Astieso) there is a small outcrop of Danian limestone by the side of a forestry track which yields *Coraster* and *Cyclaster aturicus* Seunes.

Larumbe. On the eastern side of the village of Larumbe Maastrichtian black shales crop out. These have yielded fragments of *Stegaster* and an unidentified large spatangoid. As at Sarasate, these beds are interpreted as outer shelf or shelf basin deposits. They are more or less conformably overlain by white limestones of Danian age. Near the base there are two to three 'pebbly conglomeratic' levels, followed by thick to medium-bedded strata with thin more marly joints. These then pass upwards into a more regularly alternating series of limestones and marls. *Jeronia* occurs in the conglomeratic beds along with *Echinocorys*, while *Coraster* is most common towards the top of the section.

The uppermost beds here contain numerous planktonic foraminifera. These appear very close to *Planorotalites pseudomenardii* (Bolli) and *Acarinina mckannai* (White), which indicate Zone P4 (early Late Palaeocene). The new arcestid was found in the upper marly alternations together with *Coraster*.

Casas de Oraien. This locality is placed in the middle of a wooded area some 200 m north-west of the farm buildings forming the hamlet of Oraien, which lies close to the village of Larumbe. The outcrop exposes medium-bedded, gritty calcareous sandstones in which echinoids, fragments of crinoid stems and oysters are the most common macrofaunal elements. The microfauna includes discocyclinid foraminifera indicative of a Thanetian age. The heterogeneous nature and size of the clasts, the shallow-water nature of the fossils contained and the fact that most echinoids are found chaotically in 'nests', suggest that these beds represent debris flow deposits where neritic material has been transported into a deeper part of the basin.

Aristregui. The road-cutting 500 m north of the village of Aristregui exposes a calcareous unit delimited by sharp contacts with predominantly marly levels both under and over it. A basal medium-bedded calcareous unit is followed by an alternation of marly limestones and marls, sometimes sandy, in which several intraformational conglomeratic levels occur. These beds have been dated on the basis of their microfauna as late Danian to early Thanetian (ZB 3–6) (Plaziat *et al.*, 1975). Plaziat *et al.* recorded the presence of the echinoids *Coraster beneharnicus*, *C.* cf. *sphaericus*, *Echinocorys douvillei* and *Jeronia pyrenaica* from near the base.

FAUNAL CHANGES ACROSS THE CRETACEOUS – TERTIARY BOUNDARY

The Late Cretaceous echinoid faunas from the Santander, Basque and Navarra regions of Spain are clearly very different, and were living in very different environments. Does this have any influence on the intensity of extinction suffered at the K-T boundary event?

Faunal diversity and water-depth. The faunas that we have studied come from three very different palaeoenvironments, and consequently have very different constituent species and overall diversities. The sequence at Santander was deposited in a shallow water (i.e. *ca.* 40–100 m) storm-disrupted, open-shelf environment. It contains by far the most diverse fauna (33 species), with most species coming from the shallowest facies (horizons 4 and 7/8). Not only is this habitat rich in species, but it is dominated by species of cassiduloid and regular echinoid. There are 12 regular echinoid, 9 cassiduloid, 3 holectypoid, 6 holasteroid and 3 spatangoid species.

Virtually all of the species from the carbonate platform deposits of Olagazutia are also present at Santander, but at Olazagutia fewer taxa have been recorded. These beds were probably deposited at a similar water depth, but in a more sheltered setting, with less disturbance and less clastic influx. There are just nine species from Olazagutia. This may be in part a sampling artifact (smaller outcrop area), but the paucity of regular echinoids and cassiduloids suggests that the low diversity here may be genuine and reflect a lack of shallow-water elements.

The fauna of Santander is most similar to that described from the Limburg region around Maastricht, where comparable shallow-water deposits are found. 15 out of the 27 named species and 19 out of the 26 genera recorded at Santander also occur in the Maastricht district. The genera that appear at Santander, but which are not represented in Limburg, fall into two catagories. First, there are shallow-water taxa, such as *Zuffardia*, *Clypeolampas* and *Acanthechinus*, whose distribution is primarily Tethyan, and secondly there are rare holasteroids (*Offaster* and *Galeaster*) that were primarily living in deeper-water settings and presumably near the shallow end of their range at Santander.

The shelf-basinal facies in Navarra, represented by black shale deposits, has, by comparison, a much less diverse fauna. These beds were deposited below storm wave-base, but were probably not particularly deep. They lie distal to a carbonate platform and were presumably more nutrient starved. The fauna of just six species is strikingly different to that of Santander, and only holasteroids and spatangoids are present. *Stegaster* is dominant in this environment, but not to the exclusion of other taxa.

In the truly deep-water, upper continental slope deposits of the Bidart region stegasterids (*Stegaster* and *Tholaster*) are the only echinoids present. This fauna is found elsewhere in deep-water chalks and shales from south eastern Spain, Turkey and North Africa, but is very different from the shelf chalk faunas that are found in northern Germany and Denmark. Stegasterids were specialist surface phytodetritivores.

There was thus a very clear depth control on both the diversity and composition of echinoid faunas in the late Cretaceous ocean. Shallow water faunas have high diversity, with a major component of bulk sediment feeding cassiduloids and algivorous regular echinoids. In environments below storm wave base atelostomates totally dominate and in really deep-water settings only stegasterid holasteroids, a group specialized as surface phytodetritus harvesters, existed.

Extinction levels. During the last stage of the Cretaceous 37% of echinoid genera became extinct (Jeffery & Smith, 1997, Smith & Jeffery, 1998). However, it is almost impossible to determine whether these extinctions were synchronous and instantaneous or sporadic and spread over thousands or millions of years. This is because of the serendipitous nature of the fossil record and because high resolution correlation is rarely possible in facies where echinoids are most abundant, due to the paucity of planktonic foraminifera or other biostratigraphically useful fossils. Even where we do have excellent stratigraphic control and continuous sections up to the Maastrichtian – Danian boundary, as in the Basque region (Ward & Kennedy, 1993), the raw distribution pattern of taxa can be very misleading (Marshall & Ward, 1996, Jablonski, 1996, 1997). This is in part due to sampling artefact (e.g. the Signor-Lipps effect), whereby synchronous extinction events can appear gradual due to backward smearing of last records. However, changes in facies over time can also generate misleading patterns, with local disappearance being mistaken for global extinction as organisms migrate across the shelf tracking facies shifts driven by sea-level change. For example, although *Stegaster cotteaui* appears to survive to within 40 m of the K-T boundary and then go extinct, this is not necessarily a correct interpretation for two reasons. Firstly, the sporadic occurrence of this species in the section suggests that, with more extensive sampling we might expect its true last appearance to lie closer to the K-T boundary. More importantly, the sister species to *S. cotteaui* is *Sanchezaster habanensis* Lambert, a species known from the Lower Eocene of Cuba. Therefore, the lineage must have survived the K-T boundary event somewhere in the world even though it may have become locally extinct in the Biscay region.

Extinction levels at different water depths. A total of 40 Maastrichtian, nine Danian and nine Thanetian species are recognized in this work, the majority coming from shelf platform settings (within fair-weather wave base). Just three species from the Maastrichtian shallow water fauna are known from post-Maastrichtian deposits elsewhere, while only one of six species in basinal mudstones survives and none of the continental slope species has a post-Maastrichtian record. A literal reading of the fossil record would therefore suggest that there was 90% extinction at species level.

However, sea-level changes occurring at this time resulted in major changes in the distribution of sedimentary facies across Europe. For example, no shallow water faunas of Danian age are known from Spain, carbonate platform faunas reappearing only in the late Thanetian of the Pyrenees. Clearly this creates a major sampling bias that needs to be taken into consideration when attempting to assess levels of species extinction across the Cretaceous-Tertiary boundary. For that reason survivorship of higher clades (at generic level) is likely to give a more accurate picture. Maastrichtian species that belong to genera that have no post-Maastrichtian record can be assumed to have become extinct at around the K-T boundary, whereas those with post-Maastrichtian sister groups must clearly have passed through the interval.

Of the 25 Maastrichtian shallow-water genera reported here (see Appendix), 15 are known to survive into the Tertiary (a survivorship of 60%). For comparison three of the five shelf-basinal genera survive (60%) and one of the two continental slope genera survive (50%). Two of the three surviving genera (*Cyclaster* and *Echinocorys*) in the shelf basinal environments also occur in shallow-water faunas. If these are discounted, then we have 57% survival (13 out of 23 genera) of strictly shallow-water genera, and 25% (1 out of 4 genera) of strictly deeper-water genera.

Our sparse data therefore points towards extinction being rather more intense in shelf-basinal and upper slope settings, although the small numbers make any statistical testing meaningless. The demise of the deep-water fauna is probably linked to the plankton crash known to have occurred at the end Cretaceous, since the echinoids that become extinct are all specialist deposit feeders reliant on phytodetritus. The extinction in shallow platform settings is more difficult to assess, though here again food supply may have been crucial.

Extinction levels and palaeolatitude. Some workers (e.g., Macleod

& Keller, 1994) have suggested that faunas living at high latitudes may have suffered less extinction. So, how does the pattern of extinction and survival in Spain compare with that seen at other latitudes?

At the end Cretaceous northern Spain lay at approximately 35°N palaeolatitude (based on the palaeogeographic reconstruction of Scotese *et al.*, 1989). Two other late Cretaceous echinoid faunas, lying more or less at the same palaeolongitude, have been thoroughly documented from western Europe – from the Danish basin and from the Benelux area. The Maastrichtian of the Danish basin is composed of mid-shelf chalks best exposed on the islands of Zealand, Denmark, and Rügen, North Germany. Both lay at approximately 48°N palaeolatitude. In this basin changes in lithofacies do occur across the K-T boundary, but are much less pronounced than in any other part of Europe. As a result chalk facies occur in both the Maastrichtian and Palaeocene. Thirty-six Maastrichtian echinoid species are known, of which ten (28%) survive into the Danian. At generic level 18 of the 24 Maastrictian genera found in Denmark (75%) have a post-Maastrichtian record.

The Maastrichtian of the Benelux region includes the type Maastrichtian from the Maastricht district and the richly fossiliferous Ciply deposits. This region lay at approximately 45°N palaeolatitude. The Early Maastrichtian is represented by mid-shelf chalks and shale-limestone facies while the Late Maastrichtian is predominantly composed of shallower carbonate platform facies. The Danian echinoids from the Guelhem Formation are rather unusual, being in a calcarenitic chalk facies, but dominated by distinctly shallow-water species. No Palaeocene facies comparable to the bioclastic limestones of the Maastricht Formation are found in this region. There are 54 Maastrichtian echinoid species recorded from this region (Smith & Jeffery, in press; Appendix), of which 11 continue directly into the Danian (20%). At generic level 28 of the 38 genera have a post-Maastrichtian record (74%).

If we include the Maastrichtian faunas of the eastern Pyrenees and the Alicante-Valencia basin with those described in this paper we have a total of 59 species and 43 genera from shallow, mid-shelf and deep-water settings at approximately 35° palaeolatitude. Sixteen of the 59 species (27%) and 27 of the 43 genera (63%) have a post-Maastrichtian record.

Extinction levels at all three palaeolatitudes are very similar, and survivorship at palaeolatitudes of 35° and 45–48° are not significantly different (χ^2 test $p > 0.90$) at both generic and species level. Therefore, across Europe there was no strong latitudinal gradient to end Cretaceous extinctions in echinoids.

Changes in faunal range. Maastrichtian genera that survive into the Palaeocene either continued in the same region or became locally extinct but survived elsewhere. The relative proportion of resident to emigrating lineages in an area reflects the degree to which local facies have been disrupted. If there is a significant change in facies then one might expect to see a high degree of local extinction at species level, but with many of the lineages (represented by congeneric species) continuing into the Palaeocene. Conversely, Palaeocene genera in each region can either represent resident lineages that have survived in the area, or immigrant lineages that appear in the area for the first time.

The fauna of the early Danian Geulhem Member of the Maastricht district described by Van der Ham (1988) is a striking example of how echinoid faunal ranges underwent a major reorganization after the K-T event. The Geulhem Member has just as diverse an echinoid fauna as any member of the Maastrichtian Maastricht Formation, but there are almost no species and very few genera in common between the two. A number of taxa known from the Maastrichtian of North Africa or Spain (e.g., *Gitolampas*, *Circopeltis*, *Thylechinus*, *Linthia*) appear for the first time in the Guelhem Member. Conversely, there are also a large number of genera, present in the Maastrichtian of the Maastricht area, that are found only outside that area in the Palaeocene. Clearly there was a major shift in geographical ranges at the end Cretaceous.

Faunal immigration and emigration at the end of the Cretaceous is not restricted to the Benelux region. The Appendix gives a breakdown of the composition of the surviving Maastrichtian and Palaeocene genera in terms of their geographic origin. Only approximately one-third of taxa remained resident during this period, while significant immigration and emigration from all three regions discussed above took place (Table 2). The resulting pattern of high levels of local species extinction accompanied by marked shifts in generic range appears to characterize this time interval.

Table 2 Survivorship and migration data on western European echinoid genera at the end Cretaceous. See text for explanation.

	Generic survival	Palaeocene immigrants	Resident	Maastrichtian emigrants
Denmark basin	75%	9	10	8
Benelux area	74%	7	13	15
Spain	63%	15	12	15

SYSTEMATIC DESCRIPTIONS (A.B. Smith, J. Gallemí and C.H. Jeffery)

Order **CIDAROIDA** Claus, 1880

DIAGNOSIS. Regular echinoids with simple ambulacral plating and a single large primary tubercle on each interambulacral plate.

Family **PSYCHOCIDARIDAE** Ikeda, 1936

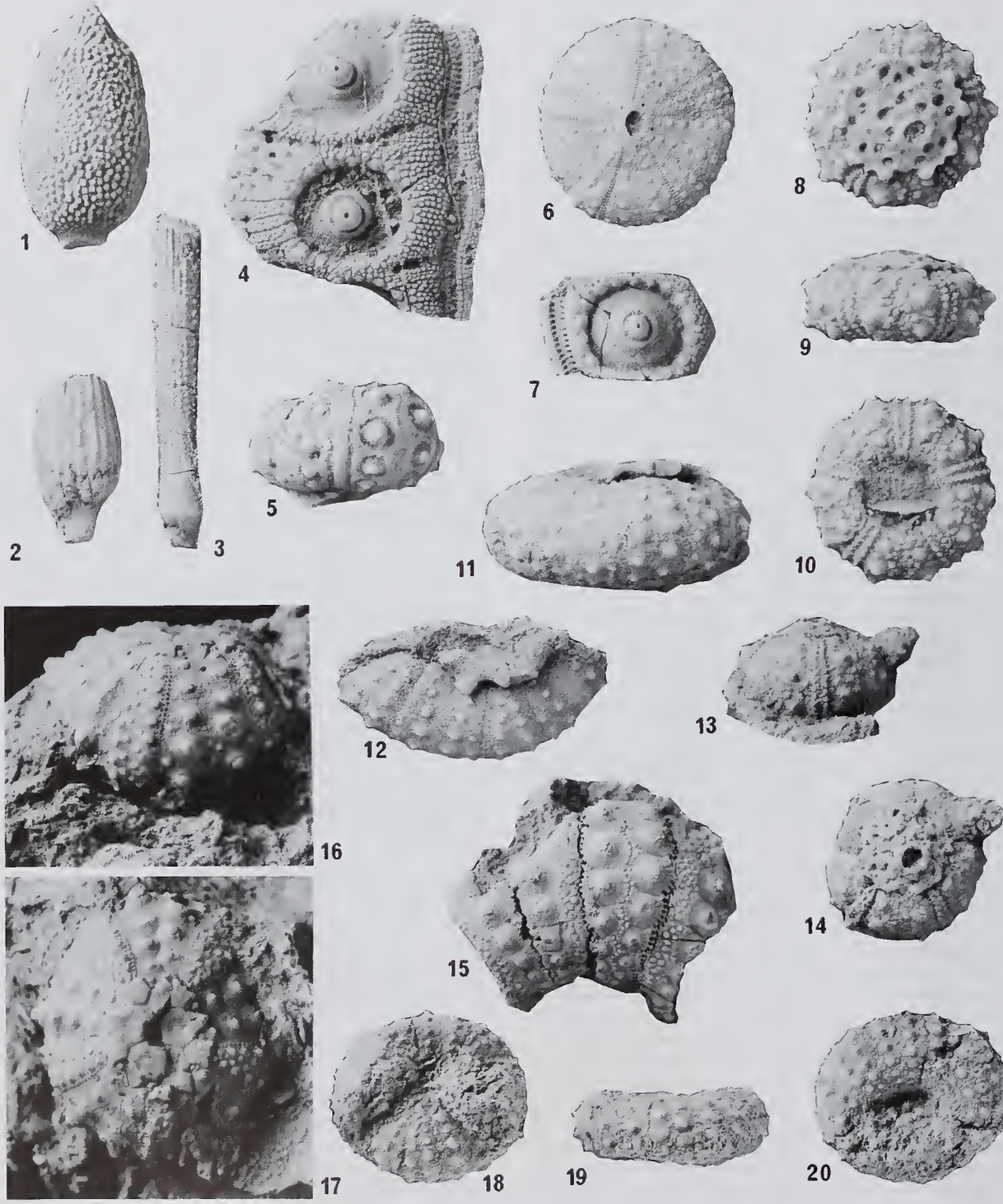
Genus ***TYLOCIDARIS*** Pomel, 1883

DIAGNOSIS. Primary tubercles imperforate, non-crenulate. Peristomial membrane contains ambulacral plates only. Primary spines clavate.

Tylocidaris (Sardocidaris) ramondi (Leymerie, 1851)
Pl. 1, fig. 1

1851 *Cidaris ramondi* Leymerie: 192, pl. 9, fig. 12 a, b, ?11c, d.
1857 *Cidaris ramondi* Leymerie; Desor: 16, pl. 6, fig. 13.
1862a *Cidaris ramondi* Leymerie; Cotteau: 315 (pars), pl. 1076, figs 1–8, 10–12, 14–17.
1910 *Tylocidaris ramondi* (Leymerie); Lambert & Thiéry: 156.

DIAGNOSIS. Test large with more than seven interambulacral plates in a column (as opposed to the five typical of *Tylocidaris (Tylocidaris)*). Ambulacra broad, with contiguous outer series of primary tubercles and inner series of three or four smaller granules in two irregular rows on each plate. Spines large, up to 25 mm in length, with a highly characteristic bulbous shaft, short neck and sharp transition to shaft. Shaft widest one-quarter of the distance above the base; width 50–60% of length. Distal end of spine bluntly pointed. Surface densely covered in coarse granules that are more or less contiguous, leaving no intergranular spaces. Granules are generally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randomly arranged, but occassionally form longitudinal lines near the distal tip.

MATERIAL STUDIED. BMNH EE4545a–h, EE6265–68, MGB 37444–49, 37480–87.

OCCURRENCE. The species is based on tests and isolated spines from the Maastrichtian of Monléon and Gensac, Haute-Garonne, French Pyrenees. In Spain spines and isolated interambulacral plates are moderately common in the Maastrichtian, horizon 6, of Olazagutia Pass, Navarra province. Lambert (1907: 712) recorded this species from 'Garumnian facies' of Bouzin (Haute-Garonne, France) which is Danian in age. This, however, is based on a test and the characteristic spines of *T. ramondi* were not apparently collected. It is not therefore certain to what species this test should be assigned.

REMARKS. A readily distinguishable species of *Tylocidaris* on account of its characteristically shaped spines and slightly greater number of interambulacral plates. The spines are readily distinguishable from those of *Tylocidaris trempinus* in both shape and ornament. Whereas *T. ramondi* spines are fat, glandiform and rapidly taper to a blunt point distally, those of *T. trempinus* are more fusiform and distally elongate, tapering to a more distinct point. More importantly, the ornament on the shaft of *T. ramondi* consists of rather fine and dense granulation that is arranged irregularly, whereas in *T. trempinus* the ornament comprises rather stout and well-formed beaded ribs, from the neck to the distal tip.

Tylocidaris (Sardocidaris) trempinus Gallemí & Smith, sp. nov. Pl. 1, fig. 2

?1851 Spines of an unknown Cidaris, Leymerie: 192, pl. 9, fig. 13.
?1862a *Cidaris ramondi* Leymerie; Cotteau: 315 (pars), pl. 1076, figs 9, 13.
1920 *Tylocidaris ramondi* Leymerie; Lambert: 4.
1992 *Sardocidaris ramondi* (Leymerie); Gallemí: 56, photo 4.

DIAGNOSIS. Spines up to 28 mm in length, fusiform, with widest part of shaft about one-third above the base. Shaft tapering to a small blunt point distally and also tapering towards the base: width less than one-third of length. No distinct handle is developed beneath the shaft. The entire shaft is ornamented with relatively stout beaded ribs, densely spaced. Base imperforate and non-crenulate.

TYPES. Holotype Universitat Autonòma de Barcelona, Palaeontological Collections PUAB-4321 illustrated by Gallemí (1977: 11, pl. 1, fig. 3); paratypes PUAB-4055 (*op. cit.* pl. 1, fig. 4) and PUAB-43626–32.

OTHER MATERIAL STUDIED. BMNH EE6114–15, MGB 37513, 37514, 37545.

OCCURRENCE. In Spain this species occurs in the Upper Campanian of Toralla, near La Pobla de Segur, Tremp Basin and Lower Maastrichtian, Serra dels Homes Morts (Salàs de Pallars) and Orcau, Tremp Basin (Gallemí, 1992). It also occurs in the Maastrichtian, horizons 4 and 6, at Santander.

REMARKS. Differs from spines of *T. ramondi* in having an ornament of continuous beaded ribs instead of dense irregular granulation. Differs from spines of *Tylocidaris clavigera* (Mantell), *T. inexspectata* Jagt & Van der Ham and *T. hemmoorensis* Salah & Schmid in its strongly fusiform and distally tapering shape. Spines of *T. baltica* are more bulbous and have only fine irregular granulation. Leymerie (1851) reported finding very occasional spines in the Maastrichtian of Monléon and Gensac, Haute-Garonne, French Pyrenees that were clearly different from those of *T. ramondi*. Although he did not name these, they appear to match those from Tremp.

Tylocidaris sp. Pl. 1, fig. 5

DIAGNOSIS. Small test approximately 17 mm in diameter and 9.3 mm in height. Peristome and apical disc similar in size, approximately 5.5–6 mm in diameter. Interambulacral zones wide with primary tubercles offset towards adradial margins. Primary tubercles imperforate, noncrenulate. Six plates in each column. Ambulacra weakly sinuous with primary tubercles to each plate and perradial granulation.

MATERIAL STUDIED. BMNH EE6109.

OCCURRENCE. Maastrichtian, horizon 2, of Santander, Cantabria.

REMARKS. The various species of *Tylocidaris* all have very similar test morphology. Without associated spines it is virtually impossible to determine such material to species level.

Family **CIDARIDAE** Gray, 1825

Genus ***TEMNOCIDARIS*** Cotteau, 1863

DIAGNOSIS. Cidaroids with perforate, non-crenulate tubercles; some fully formed adapical plates with rudimentary tubercles. Ambulacral pores non-conjugate.

Temnocidaris (Temnocidaris) magnifica Cotteau, 1863 Pl. 1, figs 3, 4

1863a *Temnocidaris magnifica* Cotteau: 357, pl. 1085, 1086.

PLATE 1

Fig. 1 *Tylocidaris (Sardocidaris) ramondi* (Leymerie, 1851), BMNH EE4545, Maastrichtian of Olazagutia Pass, Navarra. Spine, ×2.
Fig. 2 *Tylocidaris (Sardocidaris) trempinus* sp. nov., BMNH EE6114, Maastrichtian of Santander, Cantabria. Spine, ×2.
Figs 3, 4 *Temnocidaris (Temnocidaris) magnifica* Cotteau, 1863, Maastrichtian of Santander, Cantabria. **3**, BMNH EE4415, interambulacral plates and associated ambulacrum, ×2; **4**, BMNH EE6111, spine, ×2.
Fig. 5 *Tylocidaris* sp. BMNH EE6109, Maastrichtian of Santander, Cantabria. Test in profile, ×2.
Fig. 6 *Orthopsis miliaris* (d'Archiac, 1835), BMNH EE6118, Maastrichtian of Santander, Cantabria. Apical view of test, ×1.5.
Fig. 7 Indet. cidarid, BMNH EE6113, Maastrichtian of Santander, Cantabria. Interambulacral plate and associated ambulacral plates, ×2.
Figs 8–10 *Salenia (Pleurosalenia) maestrichtensis* Schlüter, 1892, BMNH EE4423, Maastrichtian of Olazagutia Pass, Navarra. Apical, lateral and oral views, ×2.
Figs 11, 12 *Acanthechinus* sp. BMNH EE6128, Maastrichtian of Santander, Cantabria. Lateral and apical views, ×2.
Figs 13, 14 *Salenia (Pleurosalenia) scabra* (Nestler, 1965), BMNH EE6110, Maastrichtian of Santander, Cantabria. lateral and apical views, ×1.5.
Fig. 15 *Phymosoma hexaporum* Lambert, 1927, MGB 37556, Maastrichtian of Santander, Cantabria. Adoral portion of test, ×2.
Figs 16, 17 *Goniopygus tetraphyma* Lambert, 1907, BMNH EE4419, Maastrichtian of Santander, Cantabria. Lateral and apical views, ×2.
Figs 18–20 *Gauthieria pseudomagnifica* (Cotteau, 1877), BMNH EE6117, Thanetian of Casas de Oraien, Navarra. Apical, lateral and oral views.

*non*1982 *Temnocidaris magnifica* Salah: 209, pl. 1, figs 1–3 [=*Stereocidaris serrata* Desor]

DIAGNOSIS. Large *Temnocidaris* with relatively fine extrascrobicular tuberculation, six abreast adradially and up to 16 abreast interradially; interambulacra with *ca.* seven plates in a column; plates almost twice as wide as tall, so that primary tubercles occupy virtually the entire plate height and scrobicular circles are tangential at the ambitus. Ambulacral plates with large primary tubercle, followed by one or two secondary tubercles and then more irregular perradial tuberculation in two rows. Pitting strongly developed both in ambulacra and in interambulacral extrascrobicular zones. Spines long, cylindrical with finely thorned ribs.

OCCURRENCE. Maastrichtian, horizons 2 and 7/8, of Santander. The species was first described from the Maastrichtian of Aurignac, Haute-Garonne, France, and is also known from Cotentin, south west France.

MATERIAL STUDIED. BMNH EE4415, EE6111.

REMARKS. This species is distinguished from the very closely related *T. danica* by its finer extrascrobicular granulation. In *T. magnifica* extrascrobicular granulation is about 67% the diameter of that in *T. danica*. Only isolated spines were found in beds at Santander which are tentatively assigned to this species because of their similarity to spines of other species of *T. (Temnocidaris)*.

Indet. cidarid plates

OCCURRENCE IN SPAIN. Maastrichtian, horizons 2, 4, 5, and 7/8 of Santander; Maastrichtian, horizon 6, of Olazagutia Pass.

REMARKS. Isolated cidaroid plates with perforate noncrenulate tubercles and narrow extrascrobicular tuberculation and belonging to at least two different taxa have been collected from the Maastrichtian of Santander and Olazagutia. This material is too fragmentary to place even to genus.

Cohort **ECHINACEA** Claus, 1876

DIAGNOSIS. Regular echinoids with keeled teeth and compound ambulacral plating.

Family **ORTHOPSIDAE** Duncan, 1889

Genus ***ORTHOPSIS*** Cotteau, 1864

DIAGNOSIS. Primary tubercles perforate and non-crenulate. Ambulacra trigeminate with acrosaleniid-style plate compounding.

Orthopsis miliaris (d'Archiac, 1835) Pl. 1, fig. 6

1835 *Cidarites miliaris* d'Archiac: 170, pl. 11, fig. 8.
1864a *Orthopsis miliaris* (d'Archiac); Cotteau, *in* Cotteau 1861a–67a: 558, pl. 1131, figs 1–16 (with full synonymies up to the date).
1895 *Orthopsis morgani* Cotteau & Gauthier: 87, pl. 14, figs 6–9.
1985 *Orthopsis miliaris* (d'Archiac); Geys: 134, pl. 5, figs 8–10.
1991 *Orthopsis miliaris* (d'Archiac); Smith & Bengtson: 30, text-fig. 23, pl. 8, figs B–F.
1995 *Orthopsis miliaris* (d'Archiac); Smith: 136, figs 12–14, pl. 2, figs 4–5; pl. 3, figs 1–9.

DIAGNOSIS. Test up to *ca.* 25 mm in diameter; depressed; rounded in profile with ambitus slightly below mid-height. Apical disc dicyclic; usually preserved in position. Ambulacra straight with uniserial columns of pore-pairs. Plating trigeminate with all three elements reaching the perradial suture; primary tubercle overlapping two of the three elements only. Interambulacra with central primary tubercle and slightly smaller secondary tubercles on adradial and interradial margins from ambital region adorally. Peristome moderately large and slightly sunken.

OCCURRENCE IN SPAIN. Maastrichtian, horizons 7/8 and 9, of Santander; Upper Campanian of Barranc de Vilanova, Toralla, near La Pobla de Segur, Tremp Basin and Lower Maastrichtian of Homes Morts Member, Salàs de Pallars, Tremp Basin (Gallemí, 1992). This species is widely distributed in the Upper Cretaceous of Europe and the Middle East (Smith & Jeffery, in press).

MATERIAL STUDIED. MGB 37563, 37564, BMNH EE6118–24.

Order **CALYCINA** Gregory, 1900

DIAGNOSIS. Regular echinoids with stout elevated cap-like apical system that incorporates one or more large suranal plates firmly bound to the ring of genital plates.

Family **SALENIIDAE** Agassiz, 1838

Genus ***SALENIA*** Gray, 1835

DIAGNOSIS. Periproct offset towards ocular I.

Subgenus ***SALENIA (PLEUROSALENIA)*** Pomel, 1883

DIAGNOSIS. Salenia with predominantly simple ambulacral plating; plating entirely simple towards peristome.

Salenia (Pleurosalenia) scabra (Nestler, 1965) Pl. 1, figs 13, 14; Fig. 6

1950 *Salenidia bonissenti* Cotteau; Kongiel: 311, 321, pl. 1, figs 1–4.
1965 *Salenidia scabra* Nestler: 987, pl. 4, figs 4–7.
1973 *Salenidia scabra* Kutscher: 111, figs 13, 14.
1975 *Salenidia scabra* Nestler: 89.
1979 *Salenidia* cf. *bonissenti* Cotteau; Geys: 890, pl. 1, fig. 4, pl. 2, fig. 2, pl. 3, figs 6–8, pl. 4, figs 1, 2.
1987 *Salenidia ?bonissenti* Van der Ham *et al.*: 21.

DIAGNOSIS. Up to 15 mm diameter; relatively tall (height *ca.* 60% test diameter). Apical disc subconical, weakly pentastellate in outline with ocular plates projecting slightly. Periproct small, trigonal, with slight lip. Large oval sutural pits at triple junctions and mid-length along all disc plate sutures; strong ridges run radially between the sutural pits giving the disc a very characteristic appearance. Ambulacra straight, unigeminate throughout (rare bigeminate elements at ambitus), with relatively wide perradial band of granulation separating primary tubercles. Five interambulacral plates in a column.

OCCURRENCE. Maastrichtian of Santander, horizon 4. Elsewhere the species is known from the late Early Maastrichtian of Rügen, Germany, Late Maastrichtian of Poland and Eben-Emael, Belgium.

MATERIAL STUDIED. BMNH EE4423a, b, BMNH EE4430, MGB 37575.

REMARKS. Separated from *S. anthophora* at comparable test diameters by having a smaller sized disc. *Salenia bonissenti* (Cotteau,

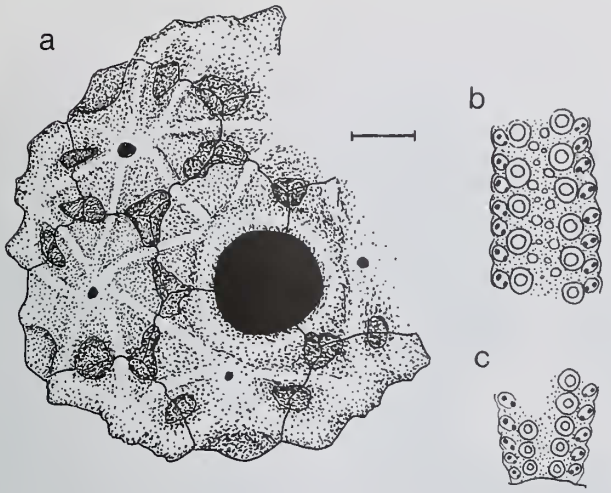

Fig. 6 Camera lucida drawings of plating in *Salenia (Pleurosalenia) scabra* (Nestler, 1965) from the coast west of Cabo Mayor (Santander, Cantabria); BMNH EE6110. **a**, apical disc; **b**, adapical ambulacrum; **c**, adoral ambulacrum, peristome at base. Scale bar = 1 mm.

1866b) has usually been treated as a distinct species characterized by having sharp carina on apical disc plates (e.g. Geys, 1979). However, Cotteau's original illustrations do not show sharp carina, only a somewhat gentle undulose plate surfaces similar to many specimens of *S. anthophora*. The oldest available name for forms with sharp carina radially arranged on genital and suranal plates is *Salenidia scabra* Nestler (1965).

Salenia (Pleurosalenia) maestrichtensis Schlüter, 1892 Pl. 1, figs 8–10

1857 *Salenia bourgeoisi* Bosquet: 3.
1862 *Salenia bourgeoisi* Cotteau, *in* Cotteau 1861a–67a: 162 (*pars*), pl. 1040, figs 25–28.
1892 *Salenia Maestrichtensis* Schlüter: 196.
1935 *Salenia bourgeoisi* Cotteau; Smiser: 26, pl. 2, fig. 7.
1979 *Salenidia maestrichtensis* Schlüter; Geys: 298, figs 1.1–1.7.
1979 *Salenidia sanctipetri* Geys: 303, figs 5.1–5.6, 6.1–6.2.
1987 *Salenidia maestrichtensis* Schlüter; Van der Ham *et al.*: 21, pl. 2, fig. 3.
1987 *Salenidia sanctipetri* Geys; Van der Ham *et al.*: 22.

DIAGNOSIS. Test generally rather small (up to about 12 mm test diameter), and depressed in profile (height *ca.* 50% of test diameter). Apical disc flat with raised margins and a small but distinct rim surrounding the periproct. Periproct in general rather small, slightly smaller than the suranal plate. Ocular plates T-shaped, projecting beyond genital plates slightly. Sutural pits large, present at all triple junctions and in addition midway along genital-ocular plate sutures; becoming quite angular in large individuals. Ambulacra straight and relatively wide, with outer columns of contiguous primary tubercles and an inner band of secondary tubercles with intervening granules. Rare bigeminate elements may be present, but for the most part ambulacra are unigeminate. Interambulacra wide with primary tubercles positioned close to the adradii, leaving a broad, somewhat depressed interradial zone of secondary granules. Primary tubercles with relatively coarse mamelons. Peristome small and somewhat invaginated.

OCCURRENCE. Spanish material comes from the Maastrichtian, horizon 6, Olazagutia Pass, Navarra province and Maastrichtian, horizon 4, Santander. The species was first described from the Late Maastrichtian Chalk of the Maastricht district, The Netherlands and Belgium, and is also reported from the Ciply Craie phosphatée and St Symphorien Gravel at Ciply, Belgium (*fide* Geys, 1979).

MATERIAL STUDIED. BMNH EE4423a, b, EE4430, MGB 37574.

REMARKS. The distinction between this species and juvenile *S. anthophora* is difficult. In both species apical disc plates are characteristically dimpled at small sizes, and it may be that the two forms cannot be separated until test sizes of about 1 cm have been reached. By this size *S. maastrichtensis* is obviously flatter and has wider and more depressed interradial bands than *S. anthophora*.

Subgenus ***SALENIA (SALENIA)*** Gray, 1835

DIAGNOSIS. *Salenia* with predominantly bigeminate ambulacral plating; plating never simple adorally.

Salenia (Salenia) sp.

DIAGNOSIS. A small individual 4.2 mm in diameter with a large apical disc with prominent sutural pits. Ambulacral plating bigeminate at ambitus and adorally.

MATERIAL STUDIED. BMNH EE4431.

OCCURRENCE. Maastrichtian, horizon 9, Santander.

REMARKS. This specimen is clearly distinct from the other saleniids described here on account of its bigeminate ambulacral plating. However, it is too small an individual to identify with confidence to species level.

Order **ARBACIOIDA** Gregory, 1900
Family **GONIOPYGIDAE** Smith & Wright, 1993

Genus ***GONIOPYGUS*** Agassiz, 1838

DIAGNOSIS. Apical disc solid and raised above the corona; no suranal plate present; genital plates pointed with gonopore opening at tip or in immediately adjacent interambulacra. Primary tubercles imperforate, non-crenulate. Ambulacral plating basically trigeminate with upper element in each triad occluded.

Goniopygus tetraphyma Lambert, 1907 Pl. 1, figs 16, 17

1907 *Goniopygus tetraphyma* Lambert: 701, pl. 25, figs 7–9.
1949 *Goniopygus jeanneti* Sánchez Roig: 54, pl. 2, figs 7, 8.

DIAGNOSIS. Test up to 25 mm diameter; subconical in profile with low ambitus and small flat summit. Apical disc solid, elevated above the corona; dicyclic, with pointed genital plates; gonopores opening at the very distal point of genital plates, beyond the elevated portion. Periproct small, trigonal, with three perianal tubercles. Ambulacra wide, trigeminate throughout with small phyllodes adorally; each plate carrying a large primary tubercle and a smaller secondary tubercle, the latter forming a distinct inner series. Interambulacra with single large primary tubercle; adapical plates lacking secondary tubercles, but those from the ambital region adorally have five or six small secondary tubercles. Peristome large, hardly sunken.

OCCURRENCE. Maastrichtian, horizon 7/8, Santander. The type of this species comes from the Upper Cretaceous of Roquefort (Haute-

Garonne, France). It is also known from the Upper Cretaceous of Cuba and from the Maastrichtian of Fígols, Llobregat River basin, Catalonia, Spain (MGB collections).

MATERIAL STUDIED. BMNH EE4419, EE6129, MGB 37576.

REMARKS. Easily distinguished from other species of *Goniopygus* by its very wide ambulacra with prominent double columns of secondary tubercles. Only the 25 mm diameter individual shows the distinct double ambulacral tubercles characteristic of this species. Two very much smaller specimens (less than 10 mm) from the same horizon are tentatively assigned to this species, although they are too small to have developed prominent secondary ambulacral tuberculation.

Order **PHYMOSOMATOIDA** Mortensen, 1904
Family **PHYMOSOMATIDAE** Pomel, 1883

DIAGNOSIS. Apical disc not firmly bound to corona; large and monocyclic, but plating usually lost. Ambulacra polygeminate with phymosomatid-style compounding. Primary tubercles imperforate and crenulate.

Genus ***GAUTHIERIA*** Lambert, 1888

DIAGNOSIS. Phymosomatids with pore-pairs uniserial throughout. One large interambulacral tubercle on ambital interambulacral plates with small adradial tubercles present on adoral plates. Peristome usually deeply sunken.

Gauthieria pseudomagnifica (Cotteau, 1877)
Pl. 1, figs 18–20

1863 *Cyphosoma magnificum* Cotteau: 185 (*nomen nudum*).
1877 *Cyphosoma pseudomagnificum* Cotteau; Cotteau: 55, pl. 4, figs 1–6.

DIAGNOSIS. Test up to 35 mm in diameter; circular in outline and depressed in profile (height about 40–50% of diameter). Apical disc opening pentagonal, relatively small (30% of test diameter). Peristome equally small and deeply invaginated. Ambulacra tapering adapically; ambital compound plate with six or seven pore-pairs defining weak arcs; pore-pairs remain uniserial throughout, with no pore-crowding adorally. Single large primary tubercle on each ambulacral and interambulacral plate. Tubercles large with circular areole and relatively small mamelons. Much smaller secondary tubercles present on adradial and interradial margins of subambital plates. Granulation outside primary tubercles rather poorly developed. Distinct interradial naked zone developed adapically.

OCCURRENCE. Our two specimens come from the Upper Thanetian, *P. pseudonenardii* Zone, limestone of Casas de Oraien, near Larumbe, Navarra, Spain. The type locality for this species is the Thanetian of Belbèze, Haute-Garonne, France. It has also been recorded from the Thanetian of Le Tuco near Cazeneuve, Haute-Garonne, France, and from the Petites Pyrenées (Plaziat *et al.*, 1975).

MATERIAL STUDIED. BMNH EE 6117, MGB 37425.

REMARKS. The arcuate uniserial arrangement of ambulacral pore-pairs distinguish this species from other phymosomatid species described here.

Genus ***DIPLOTAGMA*** Schlüter, 1870

DIAGNOSIS. Phymosomatid with biserial pore-pairs developed from the ambitus adapically and with strong adoral phyllodes. Test subconical and apical disc rather small. Interambulacral plates very wide and low with primary tubercles contiguous in column; broad granular zones developed both interradially and perradially. Tubercles imperforate and crenulate.

Diplotagma sp. Pl. 2, figs 1, 2

DIAGNOSIS. Test 37–38 mm in diameter and about 23 mm in height. Apical disc about 50% of test diameter, peristome slightly larger and a little sunken. Pore-pairs arranged biserially from the ambitus adapically but in arcs subambitally and forming phyllodes adorally. Subambital plates have five pore-pairs to a plate, adapical plates with four pore-pairs. Ambulacral tubercles are contiguous in vertical columns and are separated by a wide perradial zone of granulation. Interambulacral plates are very wide (more than three times broader than tall at the ambitus) and have a single primary tubercle. Secondary tubercles are developed adradially, one on oral plates and up to three on ambital and supra-ambital plates.

OCCURRENCE. Maastrichtian, horizon 7/8, Santander.

MATERIAL STUDIED. BMNH EE4417.

REMARKS. Our only specimen is rather badly abraded, but shows the general features of *Diplotagma*, namely the rather delicate primary tubercles and broad granular adradial and interradial zones, together with the biserially arranged pore-pairs from the ambitus to the apex. Its strongly developed adoral phyllodes distinguishes it from *Acanthechinus*. *Diplotagma* sp. nov. (Smith & Jeffery, in press), from the Upper Maastrichtian of the Maastricht area, differs from the Spanish specimen in having narrower, coarser and more heterogeneous interradial tuberculation.

PLATE 2

Figs 1, 2 *Diplotagma* sp., BMNH EE4417, Maastrichtian of Santander, Cantabria. Oral and aboral views, ×1.5.

Figs 3, 4 *Phymosoma granulosum* (Goldfuss, 1829), BMNH EE6127, Maastrichtian of Santander, Cantabria. Apical and lateral views, ×2.

Figs 5–8 *Adelopneustes ernsti* Smith & Gallemi, BMNH EE6134 (**holotype**), Thanetian of Casas de Oraien, Navarra. Apical, oral, lateral and posterior views, ×2.

Figs 9–11 *Camerogalerus cantabricus* Smith & Gallemi, BMNH EE6132 (**holotype**), Maastrichtian of Santander, Cantabria. Oral, apical and lateral views, ×5.

Fig. 12 *Coenholectypus nachtigali* (Krumbeck, 1906), BMNH EE6129, Maastrichtian of Santander, Cantabria. Apical view, ×1.5.

Figs 13–16 *'Echinogalerus' vetschauensis* (Schlüter, 1902), BMNH EE6164, Maastrichtian of Santander, Cantabria. Apical, oral, lateral and posterior views, ×3.

Figs 17–20 *Echinogalerus muelleri* (Schlüter, 1902), BMNH EE6138, Maastrichtian of Olagazutia Pass, Navarra. Apical, oral, lateral and posterior views, ×3.


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Genus ***PHYMOSOMA*** Haime, *in* d'Archiac & Haime, 1853

DIAGNOSIS. Test depressed with apical disc opening large and peristome hardly invaginated. Pore-pairs forming short phyllodes adorally and becoming biserial adapically. Primary tubercles relatively coarse, occupying most of the interambulacral plate. Tubercles imperforate and crenulate.

Phymosoma granulosum (Goldfuss, 1829) Pl. 2, figs 3, 4

1829 *Cidarites granulosus* Goldfuss: 122, pl. 40, fig. 7.
1865 *Cyphosoma granulosum* Cotteau, *in* Cotteau 1861a–67a: 684, pl. 1169.
1898b *Gauthieria broeki* Lambert: 152, pl. 4, figs 1–5.

DIAGNOSIS. Test 20–25 mm in diameter, depressed in profile with rounded ambitus. Ambulacra with five-geminate plate compounding; pore-pairs arranged in arcs on ambital plates but becoming biserial towards the apex. Large primary tubercle on ambulacral plates, separated by single band of granules on ambital plates. Short phyllodes developed adorally. Interambulacral plates a little wider than tall and dominated by a single large primary tubercle with a large mamelon. Narrow adradial and interradial bands. Peristome hardly invaginated.

OCCURRENCE. Maastrichtian, horizon 2, Santander.

MATERIAL STUDIED. BMNH EE6127.

REMARKS. Distinguished from *Diplotagma* sp. by its relatively coarse interambulacral tuberculation, the tubercles largely filling each interambulacral plate. Distinguished from *Acanthechinus* sp. in having its peristome hardly invaginated and in having obvious adoral phyllodes. *P. hexaporum* is similar, but has more pore-pairs to each ambital ambulacral plate (six or seven as opposed to five) and has distinct secondary tubercles to the adradial side of primary tubercles on ambital and supraambital plates.

Phymosoma hexaporum Lambert, 1927 Pl. 1, fig. 15; Fig. 7

1927 *Phymosoma hexoaporum* Lambert: 35, pl. 2, figs 25–27.
1928 *Phymosoma hexaporum* Lambert: 61.
1992 *Phymosoma hexaporum* Gallemí: 80, fig. 24.

DIAGNOSIS. Test relatively large and depressed, up to about 40 mm diameter (estimated). Apical disc pentagonal, peristome slightly sunken and small (about 12 mm, estimated). Ambulacral plates occupied by single large primary tubercle; areoles confluent adorally and just separated on ambital and aboral plates. Pore-pairs in arcs of six on ambital and subambital plates and forming distinct phyllodes adorally. Aboral pore-pairs presumably arranged biserially, as in the type, although none of our specimens has a well-preserved upper surface. Granulation rather sparse. Interambulacral plates distinctly wider than tall with adradial and interradial granular zones. Small secondary tubercles only very weakly differentiated adradially on adoral and subambital plates, but better developed adapically.

OCCURRENCE. Maastrichtian, horizons 4 and ?7/8, Santander. Campanian/Maastrichtian beds at Erice, Navarra.

MATERIAL STUDIED. MGB 37556, BMNH EE6126, EE4422, ?EE4416.

REMARKS. Distinguished from *Diplotagma* by its taller interambulacral plates and stouter primary tubercles, and by its uniserially arranged pore-pairs on ambital plates. It differs from *P. granulosum* in having wide zones of granulation and by having six or seven rather than five pore-pairs to each ambital ambulacral plate.

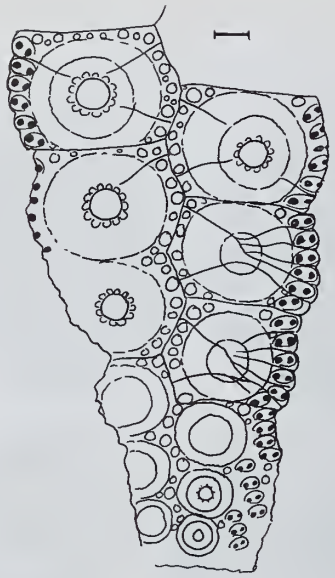


Fig. 7 Camera lucida drawing of plating in *Phymosoma hexaporum* Lambert, 1927 from the coast west of Cabo Mayor (Santander, Cantabria); MGB 37556, adoral part of an ambulacrum. Scale bar = 1 mm.

Genus ***ACANTHECHINUS*** Duncan & Sladen, 1882

DIAGNOSIS. Phymosomatid with pore-pairs arranged biserially from the ambitus aborally. Peristome deeply invaginated and pore-pairs arranged uniserially adorally without phyllodes; primary ambulacral tubercles not crowded adorally. One large primary tubercle to each interambulacral plate.

Acanthechinus sp. Pl. 1, figs 11, 12

DIAGNOSIS. Specimen between 25 and 28 mm diameter; height 9.3 mm; rounded in profile with ambitus a little below mid-height. Apical disc moderately large; peristome smaller, strongly invaginated. Ambulacra tapering adapically; pore-pairs uniserial below the ambitus but biserial from the ambitus adapically. Six or seven pore-pairs to an aboral plate, but five on ambital plates. Ambulacral plates with single large primary tubercle; tubercles separated by a single row of granules both perradially and within a single column. Tubercles remain separated towards the peristome. Eleven interambulacral plates in a column, each with a single primary tubercle. Plates wider than tall and primary tubercles confluent on ambital and adoral plates. A band of small secondary tubercles is developed along the adradial plate margin on the oral surface. On plates just above the ambitus, a distinctly enlarged secondary tubercle appears close to the adradial margin.

OCCURRENCE. Maastrichtian, horizon 2, Santander.

MATERIAL STUDIED. BMNH EE6128.

REMARKS. The deeply sunken peristome, and relatively small and wide plates, distinguish this from the two *Phymosoma* species. It resembles *Diplotagma*, but that species has shorter and wider interambulacral plates, with wider and more granular interradial and perradial bands. Furthermore, *Acanthechinus* has a deeply sunken

peristome, whereas in *Diplotagma* the peristome is hardly sunken and there are well-developed phyllodes. Lambert (1907) described a species of *Acanthechinus*, *A. savigni* (as *Phymosoma*), from the Maastrichtian of Gensac, Haute-Garonne, France. This is based on a single large individual 56 mm in diameter. This specimen has seven pore-pairs to an ambital ambulacral plate, whereas our specimen has just five. For this reason we are hesitant to unite the two. However, the number of pore-pairs associated with ambital plates does increase during growth in the closely related *A. spectabile* Cotteau & Gauthier, from the Maastrichtian of the United Arab Emirates (Smith 1995), and it is possible that the two are conspecific. More material from both populations is required, however.

Cohort **IRREGULARIA** Latreille, 1825

DIAGNOSIS. Periproct opens outside the apical disc circlet.

Order **HOLECTYPOIDA** Duncan, 1889
Family **HOLECTYPIDAE** Lambert, 1900

DIAGNOSIS. Pore-pairs undifferentiated in ambulacra. Peristome central, circular, with buccal notches.

Genus ***COENHOLECTYPUS*** Pomel, 1883

DIAGNOSIS. Holectypoids with five gonopores and test lacking internal butressing.

Coenholectypus nachtigali (Krumbeck, 1906) Pl. 2, fig. 12; Fig. 8d, e

1906 *Discoidea Nachtigali* Krumbeck: 86, pl. 7.
1907 *Holectypus proximus* Lambert: 701, pl. 25, figs 12–14.
1977 *Coenholectypus proximus* Gallemí: 62, pl. 10.
1979 *Coenholectypus proximus* Gallemí: 356, pl. 1.
1992 *Coenholectypus proximus* Gallemí: 124, figs 37, 38.

DIAGNOSIS. Test small, up to 15 mm diameter; depressed, with ambitus relatively low; lower surface rounded and sunken towards peristome. Apical disc with five gonopores; genital plate 2 is enlarged and occupies the centre of the disc; the other genital plates are reduced in size and the posterior ones are separated from one another by ocular plates. Ambulacral plating simple from apex to subambital region; trigeminate adorally; pore-pairs uniserial and undifferentiated. Periproct large, extending from close to the peristome to the ambitus, so that it is visible in posterior view. Tuberculation of interambulacral plates consists of a row of small primary tubercles, becoming offset slightly near the adradius, separated by a single dense row of miliary tubercles.

OCCURRENCE. Maastrichtian, horizons 2, 5 and 7/8, Santander. Maastrichtian, horizon 6, Olazagutia Pass, Navarra. Lower Maastrichtian of the Homes Morts Member at Sapeira and Santa Engràcia, Tremp Basin (Gallemí, 1992). The type comes from the Maastrichtian of Roquefort (Haute-Garonne), France.

MATERIAL STUDIED. BMNH EE6129–31, MGB 37499.

REMARKS. Easily distinguished from the other holectypoid found here, *Camerogalerus cantabricus* sp. nov., by the large size of its periproct and by its much lower and wider ambital plates. It also has much better aligned miliary granulation. Krumbeck (1906) erected the species *Discoidea Nachtigali* on the basis of specimens from the Maastrichtian of Libya. From the rather sketchy illustrations and description these cannot be distinguished from Lambert's species. Unfortunately, Krumbeck's types were destroyed during the Second World War and the original descriptions and figures are inadequate to be fully confident about its true identity.

Genus ***CAMEROGALERUS*** Quenstedt, 1873

DIAGNOSIS. Holectypids with internal butresses along adradial margins of interambulacral plates on oral surface. Genital plates all equal in size with madrepores generally distributed across all five plates.

Camerogalerus cantabricus Smith & Gallemí, sp. nov. Pl. 2, figs 9–11; Fig. 8a–c

TYPES. Holotype EE6132; paratype MGB37577.

DIAGNOSIS. Small, hemispherical species up to 7 mm in diameter. Circular in outline, subconical in profile (height 64% of diameter) with ambitus at about one-third test height; lower surface convex, hardly sunken towards the peristome. Apical disc with five gonopores. Ambulacra straight, with uniserial pore-pairs; plating simple above ambitus, but in triads from ambitus adorally with one and then two demiplates in each triad. Interambulacra composed of relatively tall, narrow plates. Tuberculation comprises scattered primary tubercles set amongst irregularly arranged miliary granules. Peristome very small, 1.5 mm in diameter (22 % test diameter), with feeble buccal notches. Periproct also very small and situated close to the peristome; separated by just 2 plates from the peristome; distance from periproct to ambitus is much greater than distance separating the periproct and peristome. Internal butressing narrow and blade-like and extending to the ambitus (seen on MGB 37577 where the oral surface is damaged).

OCCURRENCE. Maastrichtian, horizon 2 (paratype) and 4 (holotype), Santander.

REMARKS. Distinguished from *Coenholectypus nachtigali* by the much smaller size of its periproct, its more inflated profile and by its very different tuberculation.

Order **ECHINONEOIDA** Clark, 1925
Family **CONULIDAE** Lambert, 1911

DIAGNOSIS. Irregular echinoids with a compact apical disc with four genital plates. Ambulacra with pyrinoid plating; pore-pairs undifferentiated. Peristome small, circular to elliptical, lacking buccal notches. Tubercles small, dense, uniform and sunken.

Genus ***CONULUS*** Leske, 1778

DIAGNOSIS. Conulids with pyrinoid ambulacral plating throughout. Periproct marginal to inframarginal. Pore-pairs forming widened bands adorally.

Conulus gigas (Cotteau, 1856) Pl. 3, figs 1, 2

1856 *Echinoconus gigas* Cotteau, *in* Leymerie & Cotteau: 330.
1860 *Echinoconus gigas* Cotteau; Cotteau, *in* d'Orbigny, 1853–60: 511, pl. 994, fig. 6; pl. 995, figs 1–5.
1907 *Conulus gigas* (Cotteau); Lambert: 707.
1992 *Conulus gigas* (Cotteau); Gallemí: 146, figs 45–47.
1995 *Conulus gigas* (Cotteau); Gallemí *et al.*: 269, tab. 1.

DIAGNOSIS. Test up to 70 mm in length; width approximately 90% of length; height approximately 67% of length. Domed in profile

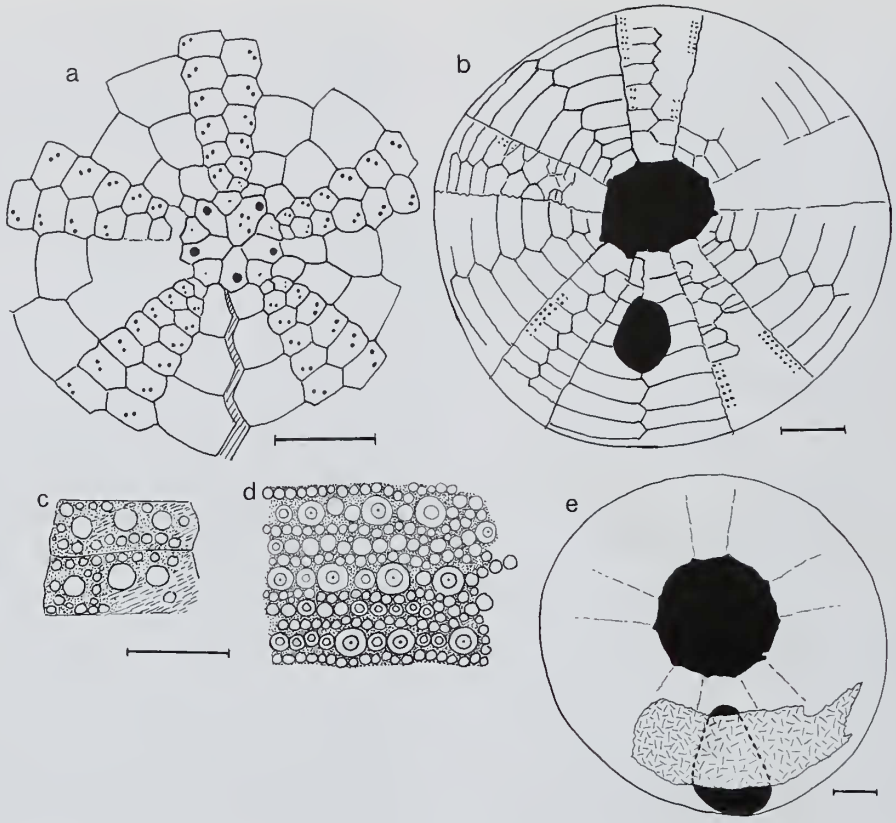


Fig. 8 Camera lucida drawing of plating: **a–c**, *Camerogalerus cantabricus* sp. nov. BMNH EE6132 (holotype); Maastrichtian, coast west of Cabo Mayor (Santander, Cantabria); **a**, apical disc; **b**, oral surface; **c**, supraambital interambulacral plates. **d, e**, *Coenholectypus nachtigali* (Krumbeck, 1906), Maastrichtian, coast west of Cabo Mayor (Santander, Cantabria); **d**, BMNH EE6129; supraambital interambulacral plates; **e**, BMNH EE6131, oral view. Scale bars = 1 mm.

with ambitus set low down. Periproct longitudinal, just subambital and clearly visible in posterior view. Oral surface pulvinate with small subcircular central peristome. Ambulacral pore-pairs forming broad bands over much of the oral surface.

MATERIAL STUDIED. BMNH EE4351–5, EE6131–33, MGB 37471, 37511, 37542, 37557.

OCCURRENCE. Maastrichtian, horizons 4, 5, 6 and 7/8, Santander. Lower Maastrichtian of the Homes Morts Member at Sapeira, Santa Engràcia and Salàs de Pallars, Tremp Basin (Gallemí, 1992). Maastrichtian, top of bed 1, Olazagutia Pass, Navarra. Maastrichtian of Mas de Santa Maria, near Ibi, Alicante province (Gallemí *et al.*, 1995). The type comes from the Maastrichtian of Saint Proupiary, near Auzas, Haute-Garonne, France and it has also been recorded from numerous other localities in Haute-Garonne, including Ausseing Massif, Picou near Roquefort, Mont Saunès, Beauchalot, Saint-Martory and Salies (Lambert, 1907).

REMARKS. Differs from *C. magnificus* (d'Orbigny) in having a longitudinal rather than transverse periproct, and from *C. douvillei* (Cotteau & Gauthier) in having a small, almost circular peristome as opposed to the distinctly oblique and large peristome of that species. This species becomes most common between levels 6 and 8 in the Maastrichtian of Santander.

PLATE 3

Figs 1, 2 *Conulus gigas* (Cotteau, 1856), BMNH EE4354, Maastrichtian of Santander, Cantabria. Oral and lateral views, ×1.

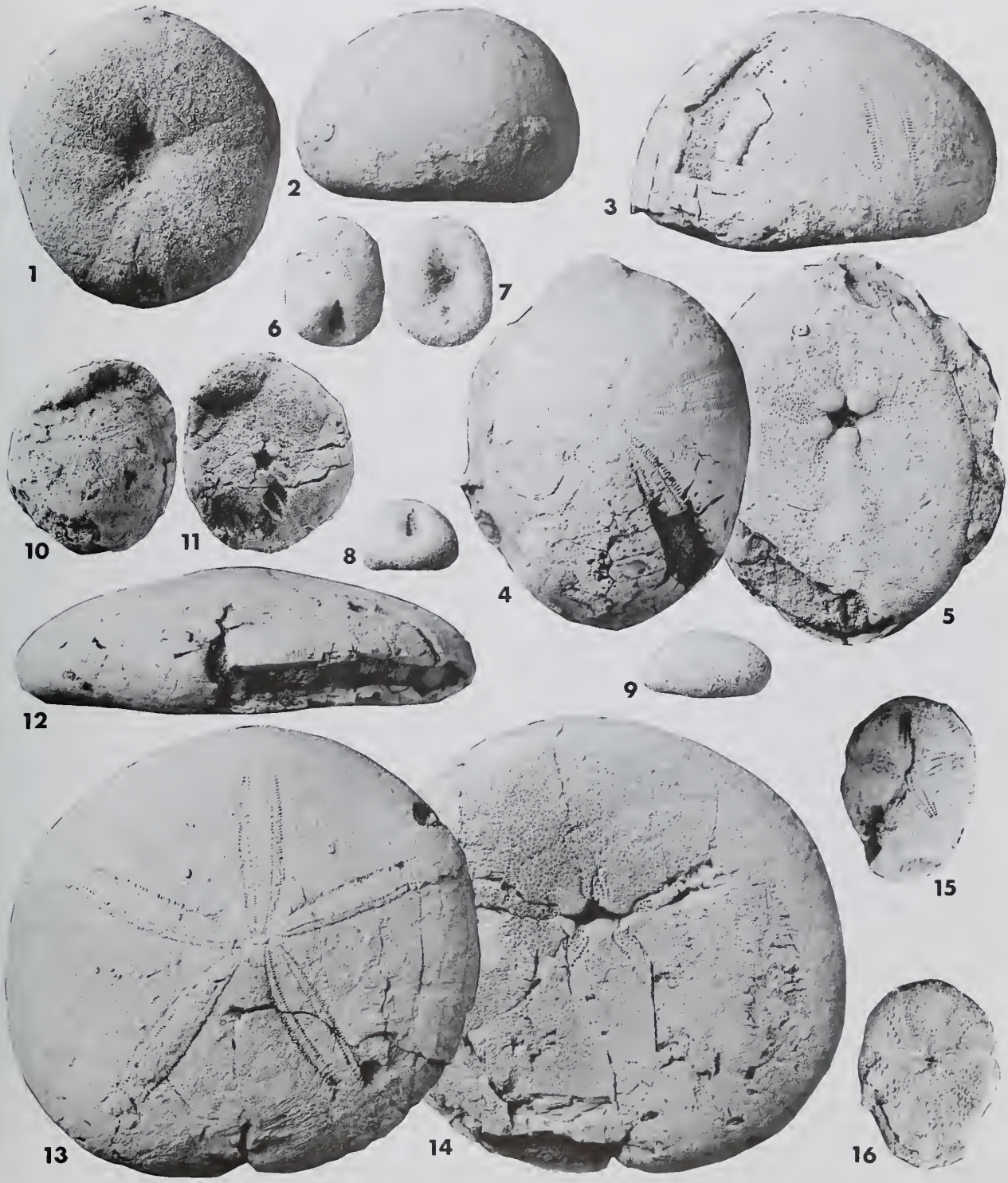
Figs 3–5 *Clypeolampas ovatus* (Lamarck, 1816), BMNH EE6144, Maastrichtian of Santander, Cantabria. Lateral, apical and oral views, ×1.

Figs 6–9 *Nucleopygus coravium* (Agassiz, *in* Agassiz & Desor, 1847), BMNH EE6148, Maastrichtian of Santander, Cantabria. Apical, oral, posterior and lateral views, ×3.

Figs 10, 11 *Zuffardia* sp., BMNH EE6153, Maastrichtian of Santander, Cantabria. Apical and oral views, ×1.5.

Figs 12–14 *Gitolampas subrotundus* (Cotteau, 1856), BMNH EE6173, Thanetian of Santander, Cantabria. Posterior apical and oral views, ×1.

Figs 15, 16 *Rhyncholampas macari* (Smiser, 1935), MGB37512, Maastrichtian of Santander, Cantabria. Apical and oral views, ×1.5.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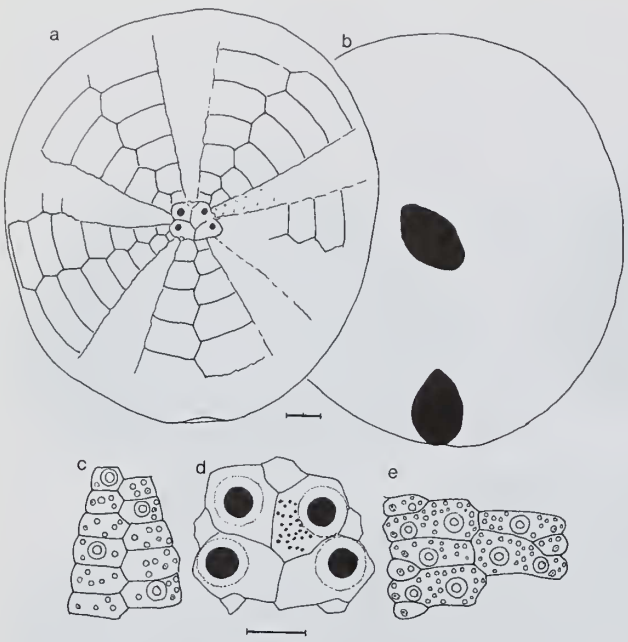

Fig. 9 Camera lucida drawings of plating in *Adelopneustes ernsti* sp. nov. from Casas de Oraien (Navarra); BMNH EE6134, **a**, apical surface; **b**, oral surface; **c**, adapical ambulacrum; **d**, apical disc; **e**, subambital ambulacrum. Scale bars: a, b = 2 mm; c–e = 1 mm.

Genus ***ADELOPNEUSTES*** Gauthier, 1889

DIAGNOSIS. Conulids with pyrinoid ambulacral plating orally and simple plating aborally. Peristome subcircular to weakly elliptical.

Adelopneustes ernsti Smith & Gallemí, sp. nov.
Pl. 2, figs 5–8; Fig. 9

DIAGNOSIS. Test ovate in outline, slightly pointed to rear; 26 mm in length, slightly narrower than long; low-domal in profile, with test height 14.5 mm. Apical disc tetrabasal with large gonopores surrounded by rims (female character only?); subcentral on genital plates. Ambulacral pores very small and rudimentary, almost impossible to see even under magnification; double adapically. Ambulacral plating apparently simple aborally; plating adorally not visible. Peristome oblique (crushed in the only specimen known), elongate towards anterior left. Lower surface strongly rounded. Periproct elongate and pointed both adorally and adapically, visible from beneath and posteriorly; as large as mouth.

OCCURRENCE. Upper Thanetian, *P. pseudomenardii* Zone, Casas de Oraien, Larumbe, Navarra province, Spain.

TYPES. Holotype, BMNH EE6134.

REMARKS. Differs from *N. boehmi* (Neitsch) in having a more depressed profile and larger gonopores surrounded by a raised platform. Differs from *N. montainvillensis* (Sorignet) in having an oblique rather than circular peristome. Differs from both these species and from all others assigned to this genus in having rudimentary aboral pores.

Order **CASSIDULOIDA** Claus, 1880

DIAGNOSIS. Peristome small, lacking buccal notches; interambulacra undifferentiated. Ambulacral pores differentiated into aboral petals and oral phyllodes, though occasionally rudimentary throughout.

Family **PLACHIOCHASMIDAE** Smith & Jeffery, in press

Genus ***ECHINOGALERUS*** König, 1825

DIAGNOSIS. Peristome small, anterior of centre. Periproct slightly wider than long, inframarginal. Petals and phyllodes rudimentary.

Echinogalerus muelleri (Schlüter, 1902)
Pl. 2, figs 17–20; Fig. 10b, d

1902 *Caratomus Muelleri* Schlüter: 316, pl. 11, figs 14–17.
1927 *Echinogalerus belgicus* Lambert: 38.
1987 *Echinocyamus muelleri* Schlüter; Van der Ham *et al.*: 28, pl. 9, fig. 3.
1992 *Echinogalerus muelleri* Schlüter; Van der Ham & Van Birgelen: 149, pl. 3, fig. 7.
1992 *Echinogalerus belgicus* Gallemí: 170, photo 6.

DIAGNOSIS. Test up to 15 mm in length; width about 85–90% of length; height about 60% of test length. Ovate in outline with rounded anterior and widest point slightly posterior to midlength. Depressed in profile with rounded margins; lower surface strongly pulvinate and slightly sunken towards peristome; upper surface depressed. Ambulacra composed entirely of simple plating; ambulacral pores double throughout, almost subpetaloid adapically in largest individuals; uniserial adorally. Pore-pairs oblique and strictly uniserial towards the peristome; widely separated. Peristome slightly anterior of centre; relatively large (13% of test length); oblique along 3-V axis. Periproct subambital, clearly visible in oral view; transverse, wider than the peristome, subtrigonal and pointed adorally; separated from the peristome by about 4 interambulacral plates. Tuberculation of scattered sunken tubercles.

OCCURRENCE. Maastrichtian, horizons 3 to 6, Santander, Cantabria; Maastrichtian, horizon 6, Olazagutia Pass, Navarra province. Lower Maastrichtian, Homes Morts Member, Salàs de Pallars and Sapeira, Tremp Basin (Gallemí 1992). The type comes from the Upper Maastrichtian of Vetschau, near Aken, Germany.

MATERIAL STUDIED. BMNH EE4412(a–d), EE4413(a–f), EE6137–38, EE6163; MGB 37451–57, 37490–98, 37500–02, 37526, 37528, 37532, 37537, 37546.

REMARKS. Similar in shape to *E. belgicus*, but with double pores in its ambulacra. Differs from *E? vetschaupensis* in having a larger peristome, more pulvinate lower surface and strictly uniserial pore-pairs adorally. Populations from Tremp and from Olazagutia Pass contain both large and small individuals, and are assigned to this species without doubt. However, only small individuals have so far been found at horizons 3 and 5 at Santander. Because these are indistinguishable from small individuals that we have from Olazagutia, we have included them in this species.

Echinogalerus? vetschauensis (Schlüter, 1902)
Pl. 2, figs 13–16; Fig. 10a, c

1902 *Caratomus vetschauensis* Schlüter: 318, pl. 11, figs 10–13.
1987 *Echinogalerus vetschauensis* Schlüter; Van der Ham *et al.*: 28, pl. 9, fig. 5.

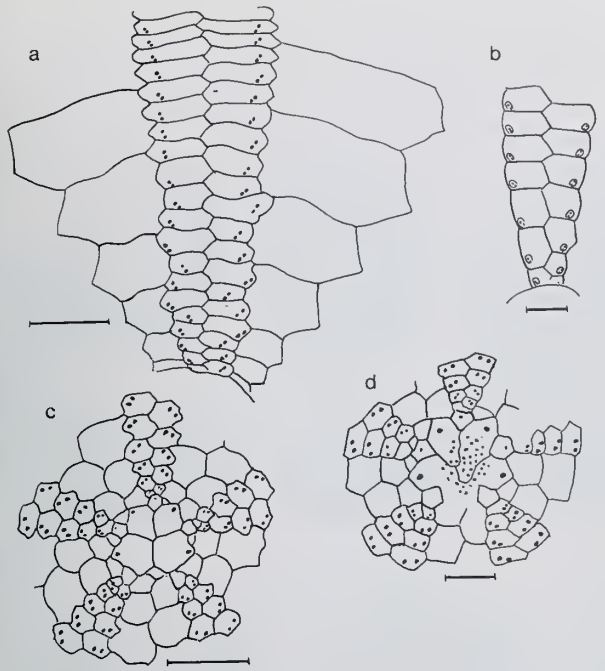

Fig. 10 Camera lucida drawings of plating in *Echinogalerus* species. **a, c**, *?E. vetschauensis* (Schlüter, 1902) from the Maastrichtian of the coast west of Cabo Mayor (Santander, Cantabria); **a**, BMNH EE6164, adoral ambulacrum, peristome opening at base; **c**, BMNH EE 6165, apical disc; **b, d**, *E. muelleri* (Schlüter, 1902), BMNH EE4412a from Olazaguti pass, Navarra; **b**, adoral ambulacrum I, peristome margin at base; **d**, apical disc. Scale bars = 1 mm.

DIAGNOSIS. Test up to 12 mm, width *ca.* 95% of length, height *ca.* 60% of length. Outline ovate with widest point at midlength; depressed in profile, with relatively flat base. Apical disc tetrabasal with posterior genital plates abutting. Ambulacra narrow; pores double aborally, but small, oblique and widely spaced; pores uniserial except adorally where they are arranged into oblique arcs of three. All ambulacral plating simple. Peristome small (6–7% of test length along the anterior-posterior axis); slightly oblique. Periproct subambital, transverse and trigonal; only slightly larger than the peristome in length, but considerably wider. Tuberculation relatively dense over the oral surface.

OCCURRENCE. Maastrichtian, horizons 2 and 4, Santander. The type comes from the Upper Maastrichtian of Vetschau, near Aken, Germany. It is also known from the Kurade limestone facies, Upper Maastrichtian of the Maastricht region.

MATERIAL STUDIED. BMNH EE6134–36, EE6164–66, MGB 37522.

REMARKS. Distinguished from *E. muelleri* by its flatter lower surface, its much smaller peristome and by having pore-pairs offset into triads towards the peristome. These features also separate *E? vetschauensis* from *E. belgicus*, but in addition, *E. belgicus* (at least as interpreted in Van der Ham *et al.*, 1987) has rudimentary aboral pores aborally that appear to be single.

This species bears a strong resemblance to *Galerites sulcatoradiatus* (Goldfuss), a species that grows to much greater size. Both have offset pore-pairs adorally and both have a similar small peristome and periproct. With further study, and better and more diverse material, *E? vetschauensis* may turn out to be simply small individuals of *G. sulcatoradiatus*.

Family **ECHINOLAMPADIDAE** Gray, 1851

Genus ***GITOLAMPAS*** Gauthier, 1889

DIAGNOSIS. Ovate to subpentagonal in outline; oral surface planar; margins rounded; upper surface planar to low subconical. Apical system tetrabasal or monobasal, anterior of centre, with four gonopores. Periproct longitudinal; opening on posterior surface within shallow sulcus. Petals subparallel, open distally; pore columns subequal. Peristome anterior, pentagonal, transverse, with vertical-walled vestibule. Phyllodes moderately well developed, with an outer and inner series of pores, the outer series being slightly bowed. No bourrelets. Basicoronal interambulacral plates wider than long. Buccal pores present. A narrow zone free of primary tubercles runs along the interradial suture between the peristome and posterior border.

Gitolampas subrotundus (Cotteau, 1856)

Pl. 3, figs 12–14

1856 *Pygorhynchus subrotundus* Cotteau, *in* Leymerie & Cotteau: 334.
1857 *Echinanthus subrotundus* Desor, *in* Desor 1855–58: 293.
1888 *Echinanthus subrotundus* Desor; Cotteau, *in* Cotteau 1885a–89a: 586, pls 173, 174, pl. 175, figs 1–3.
?1908 *Echinanthus arizensis* Cotteau; Lambert: 366.
1908 *Echinanthus Heberti* Cotteau; Lambert: 367.
?1908 *Echinanthus Cotteaui* Hébert; Lambert: 368.
1908 *Echinanthus Gourdoni* Cotteau; Lambert: 368.
1975 *Echinanthus arizensis* Lambert; Plaziat *et al.*: 631, pl. 2, figs 1, 3.

DIAGNOSIS. Test up to 87 mm in length; width 85–95% of length, height *ca.* 30–36%. Outline subcircular to weakly ovate and somewhat pointed at the posterior; lower surface relatively flat or slightly sunken towards the peristome, with rounded margins. Upper surface low domal. Apical system obscured in our specimens, but probably monobasal; lying 40% test length from the anterior border. Petals well developed, extending most of the distance to the ambitus in plan view; equally wide with interporal zone twice the width of the pore zone; open distally. Anterior petal extending 75–80% the distance to the ambitus in plan view, posterior petals extending 70–80% the distance. Peristome 40% test length from the anterior; strongly transverse and pentagonal. Phyllodes moderately well developed consisting of an outer series of *ca.* nine pores and inner series of two or three pores. Buccal pores present at outer margin of vestibular entrance to peristome.

OCCURRENCE. Upper Thanetian, *P. pseudomenardii* Zone, horizon 10, Santander. Also known from Lower Thanetian to Lower Ypresian localities in the French and Spanish Pyrenees and the Villarcayo basin (Burgos province, northern Spain). The type (Leymerie collection, Toulouse) comes from the 'Montian' of Fabas (Ariège, France), and it is also known from several other localities in Ariège (Sabarat, le Mas-d'Azil, Campagne, Montardit, Camarade and Saint-Jean-de-Verges) and Haute-Garonne (Martres, Saint-Marcet, Aurignac, Montbrun, Marsoulas).

MATERIAL STUDIED. BMNH EE6173, MGB 37573.

REMARKS. This species is easily distinguished from others

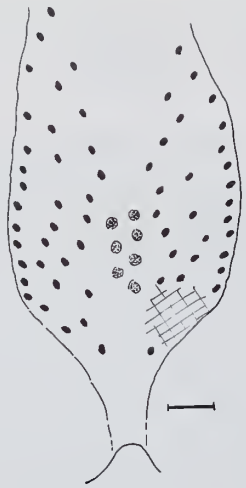

Fig. 11 Camera lucida drawing of plating in *Clypeolampas ovatus* (Lamarck, 1816) from the Maastrichtian of the coast west of Cabo Mayor (Santander, Cantabria); BMNH EE6144, phyllode of ambulacrum II, peristome margin at base. Scale bar = 1 mm.

reported here, by its large size, strongly transverse peristome and posterior longitudinal periproct. There are many species of *Gitolampas* recognized from the Maastrichtian and Palaeocene (Smith & Jeffery, in press). It is distinguished from the closely similar *G. ataxensis* (Cotteau) by the form of its petals, which are more bowed and proportionally longer than in *G. ataxensis*.

Family **CLYPEOLAMPADIDAE** Kier, 1962

Genus ***CLYPEOLAMPAS*** Pomel, 1869

DIAGNOSIS. Test with flat base and highly vaulted upper surface. Petals long, extending almost to the ambitus; slightly expanding and widely open distally. Periproct submarginal at rear of oral surface; transverse. Narrow granular sternal zone present behind periproct. Phyllodes widely expanded, with many pores scattered between the inner and outer series. Interambulacra swollen towards peristome with 'bourrelets' composed of many small plates rather than just a single large basicoronal plate.

Clypeolampas ovatus (Lamarck, 1816)
Pl. 3, figs 3–5; Fig. 11

1816 *Galerites ovatus* Lamarck, 1816: 22.
1829 *Clypeaster leskei* Goldfuss, 1829: 132, pl. 42, fig. 1.
1920 *Clypeolampas leskei* Goldfuss; Lambert: 21.
1996 *Clypeolampas* cf. *ovatus* (Lamarck); Wilmsen *et al.*: fig. 7.

DIAGNOSIS. As for genus.

OCCURRENCE. Maastrichtian, horizons 1, 2 and 4, Santander; Maastrichtian, Somo Beach, near Santander, Cantabria province. Upper Campanian of Barranc d'en Jaume, Quatretonda and Nicolasa quarry, Tavernes, Valencia province, Spain (Nicklès 1892). This species is widely reported from the Maastrichtian of the Anglo-Paris Basin, Charente-Maritime and Dordogne, France.

MATERIAL STUDIED. BMNH EE6144–47.

REMARKS. This species is moderately common in the shallowest limestones at the base of the transgressive Maastrichtian sequence at Santander. Several species have been distinguished by Lambert (1920) on material from the Santander region. The differences between his species *C. mengaudi*, *C. douvillei* and *C. ovatus* are based on the disposition of pores in the phyllodes. Although there are certainly slight differences, it is not at all clear how much individual variation exists in this character within single populations, and the three taxa may well turn out to be conspecific.

Unnamed Family

Genus ***NUCLEOPYGUS*** Agassiz, 1840

DIAGNOSIS. Subquadrate in outline and depressed in profile, with supramarginal periproct opening into subanal sulcus. Apical disc tetrabasal. Ambulacra subpetaloid at most. Peristome lacking bourrelets; perioral tuberculation confined to peristomial well. Phyllodes generally rather undeveloped with every third pore-pair insert.

Nucleopygus coravium (Agassiz, *in* Agassiz & Desor, 1847) Pl. 3, figs 6–9; Pl. 4, figs 7–9

1847 *Nucleopygus cor avium* Agassiz; Agassiz & Desor: 152.
1898b *Nucleopygus coravium* Lambert: 168, pl. 5, figs 1–4, 8–14.
1935 *Nucleopygus coravium* Smiser: 52, pl. 5, fig. 1.
1987 *Nucleopygus coravium* Van der Ham *et al.*: 29, pl. 11, fig. 2.

DIAGNOSIS. Small species, rarely reaching more than 10 mm in length; width *ca.* 75% of length; depressed with height *ca.* 50% of length. Ovoid in outline with a rounded anterior and slightly truncated posterior; widest point posterior of centre. In posterior profile the test is strongly concavo-convex. Apical system anterior, about one-third of test length from the anterior; tetrabasal with posterior genital plates not separated by the madreporite; genital plate 3 smaller than the remainder. Petals small and rudimentary, particularly the anterior petal; lateral and posterior petals equally developed, the posterior pair ending well before reaching the level of the periproctal opening. Pore-pairs weakly conjugate with equal-sized pores. Peristome large, oval to subpentagonal, slightly anterior of centre, depressed with inwardly sloping margins. Phyllodes more or

PLATE 4

Figs 1–6 *Nucleopygus scrobiculatus* (Goldfuss, 1829), Maastrichtian of Santander, Cantabria. **1**, BMNH EE6157; apical view, ×2. **2–4**, BMNH 6156; oral, lateral and posterior views, ×2. **5**, **6**, BMNH EE6154; oral and posterior views, ×2.

Figs 7–9 *Nucleopygus coravium* (Agassiz, *in* Agassiz & Desor, 1847), BMNH EE4403, Maastrichtian of Olazagutia Pass, Navarra. Apical, lateral and oral views, ×3.

Figs 10–13 *Offaster leymeriei* Cotteau, 1887, BMNH EE6170, Maastrichtian of Santander, Cantabria. Apical, oral, lateral and posterior views, ×1.5.

Figs 14–18 *Galeaster bertrandi* Seunes, 1889, BMNH EE6188, Maastrichtian of Santander, Cantabria. Apical, oral, posterior, anterior and lateral views, ×2.

Fig. 19 *Cardiaster* sp. BMNH EE6174, Thanetian of Casas de Oraien, Navarra. Oral view, ×1.

Figs 20–22 *Echinocorys scutata* forma *cotteaui* Lambert, 1903, BMNH EE6189, Thanetian of Casas de Oraien, Navarra. Oral, lateral and apical views, ×1.


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less uniserial to peristome, with no pore crowding whatsoever. Small buccal pores are present at the peristomial margin. Periproct oval, longitudinal, in distinct anal sulcus opening closer to the posterior margin than the apical system.

OCCURRENCE. Maastrichtian, horizon 2 (top) and 4, Santander; Maastrichtian, horizon 6, Olazagutia Pass, Navarra province. This species also occurs in the upper Lower to lower Upper Maastrichtian of the Maastricht district, The Netherlands and Belgium (Van der Ham *et al.*, 1987), the Maastrichtian 'Craie phosphatée' at Ciply, Belgium (Lambert, 1898b) and the Maastrichtian at Fresville, Manche, France (Lambert collection).

MATERIAL STUDIED. BMNH EE4403, EE6148–49, MGB 37519.

REMARKS. This is a small species of juvenile appearance (simple short petals, simple phyllodes, absence of bourrelets). There are several names available for such forms, but they lack distinctive characters and are virtually impossible to separate. Consequently, we group all together here under the name *N. coravium* Defrance.

This species is readily distinguished from the co-occurring *N. scrobiculatus* by its shape, which is much less tumid and with a deeply sunken oral surface, and by its phyllodes, which are completely undifferentiated. It differs from *N. geayi* in having a more posterior periproctal opening.

Nucleopygus scrobiculatus (Goldfuss, 1829)

Pl. 4, figs 1–6; Fig. 12

1829 *Nucleolites scrobiculatus* Goldfuss: 138, pl. 43, fig. 3.
1935 *Lychnidius scrobiculatus* (Goldfuss); Smiser: 49, pl. 4, fig. 10.
1957 *Nucleopygus scrobiculatus* (Goldfuss); Engel & Meijer: 88, pl. 1.
1987 *Nucleopygus scrobiculatus* (Goldfuss); Van der Ham *et al.*: 30, pl. 11, fig. 3.

DIAGNOSIS. Test up to 26 mm in length, ovate; width 85–90% of length, widest centrally; height 60–65% of length, tallest behind apical disc. Apical disc a little anterior of centre (40% of length); tetrabasal with four gonopores. Petals subequal with almost parallel columns. Periproct supraambital, but positioned far to the posterior on the steeply sloping posterior face; longitudinal with anal sulcus only pronounced in juveniles. Oral surface strongly pulvinate with peristome deeply invaginated. Peristome transverse and rounded pentagonal. Phyllodes hardly expanded adorally, with a single series of pores, becoming offset close to the peristome in specimens up to 15 mm length; with one pore in each of the first two groups of three insert in larger individuals. Peristome with deep tuberculate vestibule leading into peristome; buccal pores near top of this vestibule. No bourrelets. Narrow granular tubercle-free zone present posterior to the peristome.

OCCURRENCE. Maastrichtian, horizon 4, Santander; Maastrichtian, horizon 6, Olazagutia Pass, Navarra.

MATERIAL STUDIED. BMNH EE6154–61, MGB 37458, 37517

REMARKS. We have slight reservations about uniting our material with *N. scrobiculatus*. The holotype of *N. scrobiculatus* was established for a 7 mm individual. Later additional specimens were described by Engel & Meijer (1957) and Van der Ham *et al.* (1987) up to 21 mm in length. Small individuals from Santander and Olazagutia correspond very closely with the Maastricht population. However, larger specimens become progressively less similar, showing a less pulvinate lower surface, more rostrate posterior and phyllodes with more offset pores. When we consider the full range of sizes present at Santander, there is no clear-cut separation between the smaller and larger individuals. We therefore conclude that the small differences are growth-related and that all our material belongs to the same species.

Fig. 12 Camera lucida drawing of plating *in Nucleopygus scrobiculatus* (Goldfuss, 1829) from the coast west of Cabo Mayor (Santander, Cantabria); BMNH EE6154, phyllodes and peristome margin. Scale bar = 1 mm.

This species differs from *N. coravium* in having the periproct positioned on the steeply sloping part of the test, much closer to the posterior margin, in being much more pulvinate with a more rounded ambitus, and in lacking a strong saggital depression on its oral surface.

Family **CASSIDULIDAE** Agassiz & Desor, 1847

Genus ***OOLOPYGUS*** d'Orbigny, 1856

DIAGNOSIS. Elongate cassiduloids with flat base and subcentral, pentagonal peristome surrounded by weak bourrelets, and widened phyllodes comprising inner and outer series. Apical disc with three gonopores, no gonopore present in anterior left portion of disc. Petals rudimentary to poorly developed. Broad pitted tubercle-free zone present both anterior and posterior to the peristome.

Oolopygus sp. Fig. 13a

OCCURRENCE. Maastrichtian, horizon 5, Santander.

MATERIAL STUDIED. BMNH EE6169.

REMARKS. Our solitary specimen is a small individual just under 10 mm in length. It is too small to be identified with certainty to species level, but has sufficient characters to be confident about its generic identity. Specifically, it possesses only three large gonopores, and the oral surface is flat with a small subcentral mouth. Bourrelets are small but distinct, and a granular naked zone is developed on the oral surface. It may be a juvenile individual of *O. pyriformis* (Lamarck), the Maastrichtian species that is found in the Maastricht area. However, at this size it also bears close resemblance to *Oolopygus rostriformis* (Kadilnikova & Moskvin) from the Palaeocene of Mangyshlak, Kazakhstan.

Genus ***RHYNCHOPYGUS*** d'Orbigny, 1856

DIAGNOSIS. Small cassiduloids with a flat base and low domal profile. Peristome small, subcentral, surrounded by weak bourrelets

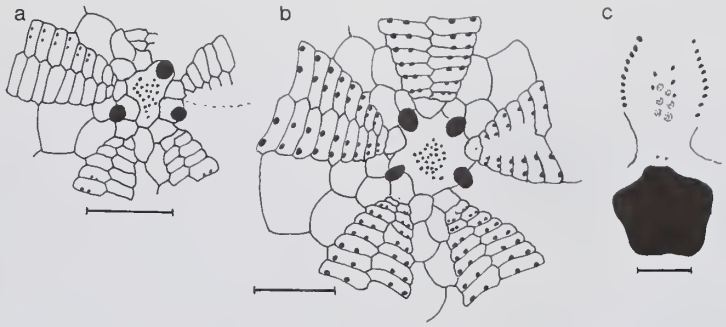

Fig. 13 Camera lucida drawings of plating in *Oolopygus* sp. and *Zuffardia* sp. from the Maastrichtian of the coast west of Cabo Mayor (Santander, Cantabria); **a**, *Oolopygus* sp., BMNH EE6169, apical disc; **b**, **c**, *Zuffardia* sp., BMNH EE6153; b, apical disc; c, phyllode and peristome margin. Scale bars = 1 mm.

and with V-shaped phyllodes comprising a single series of pores. Periproct supra-ambital, on the underside of a large lobate projection; opening appears wide and slit-like in posterior profile. Oral tuberculation arranged with a strong bilateral symmetry.

Rhynchopygus sp.

OCCURRENCE. Maastrichtian, horizon 4, Santander

MATERIAL STUDIED. BMNH EE6162.

REMARKS. Our record is based on a single specimen, representing the posterior portion of a test. This shows the highly characteristic lobe-like projection above the wide and slit-like periproctal opening. There are two species of *Rhynchopygus*, *R. marmini* (Agassiz) and *R. donetzensis* (Faas), differing primarily in the development of their petals. As our specimen does not show the petals, it cannot be assigned to species level.

Genus ***RHYNCHOLAMPAS*** Agassiz, 1869

DIAGNOSIS. Small cassiduloids with a flat base and ovate outline. Peristome small, subcentral, weakly transverse to as wide as long; rim of peristome hardly swollen; deep well leading into peristomial opening. Periproct supra-ambital; transverse, hardly sunken.

Rhyncholampas macari (Smiser, 1935) Pl. 3, figs 15, 16

1935 *Rhynchopygus macari* Smiser: 63, pl. 6, fig. 6.
1987 *Procassidulus macari* (Smiser); Van der Ham *et al.*: 30, pl. 11, fig. 6.

DIAGNOSIS. Test up to 33 mm in length; elongate with flat base and depressed upper surface. Width 75–80% of length, widest posterior of mid-length; height no more than 35% of length. Apical disc a little anterior of centre, with four gonopores; probably tetrabasal, but plating not seen. Petals well-developed, bowed and converging distally; posterior petals shorter than lateral and anterior petals. Peristome slightly anterior of centre; small and pentagonal; almost as wide as long; surrounded by small but distinctly swollen bourrelets. Phyllodes composed of a V-shaped outer series of pores plus one or two inner pores near the apex of the V. Broad pitted sagittal zone free of tubercles both anterior and posterior to the peristome. Periproct supramarginal; transverse, with slight aboral canopy.

OCCURRENCE. Maastrichtian, bed 4, Santander. This species also occurs in the Lichtenberg Horizon, and Nekum and Meerssen Members, Maastricht Formation, *B. junior* and *B. kazimiroviensis* Zones, Upper Maastrichtian of the Maastricht district, The Netherlands and Belgium (Van der Ham *et al.*, 1987).

MATERIAL STUDIED. BMNH EE6150–52, MGB 37512

REMARKS. Although our material is unfortunately rather crushed, all relevant plating details are seen, allowing us to be confident in our determination. No other cassiduloid described herein has a transverse periproct situated supra-ambitally.

Family **FAUJASIIDAE** Lambert, 1905

Genus ***ZUFFARDIA*** Checchia-Rispoli, 1917

DIAGNOSIS. Globose cassiduloids with monobasal apical disc and relatively short petals. Peristome small, subcentral, pentagonal, surrounded by distinct phyllodes and bourrelets. Periproct posterior, hardly invaginated. All pores below petals single.

Zuffardia sp. Pl. 3, figs 10, 11; Fig. 13b, c

DIAGNOSIS. Test up to 25 mm in length; almost subcircular in outline, inflated in profile with flat to weakly convex base and subcentral peristome. Apical disc compact, with four gonopores. Petals relatively short and weakly bowed; extending about half the distance to the ambitus. Peristome small, pentagonal, surrounded by small bourrelets. There is a deep well leading into the peristomial opening. A broad naked pitted zone is developed both anterior and posterior to the peristome on the oral surface. Periproct posterior, subcircular, hardly invaginated. Phyllodes well developed with bowed outer series of ten pores separated from three inner series pores. All pores single below the petals.

OCCURRENCE. Maastricthian, horizon 4, Santander.

MATERIAL STUDIED. BMNH EE6153, MGB 37521, 37525, 37527.

REMARKS. Resembles *Catopygus fenestratus* Agassiz & Desor in general appearance, but distinguished from that species by having entirely single pores below the petals, and in having a well-developed anterior and posterior naked zone that is pitted. This latter feature distinguishes it from the type species *Z. morgani* (Cotteau & Gauthier), which has an unpitted naked zone adorally. Very similar material was described from the Late Maastrichtian, *B. kasimiroviensis* Zone of Mangyshlak by Jeffery (1997). Our speci-

mens are, however, too poorly preserved to form the basis for formally erecting a new species name.

Order **HOLASTEROIDA** Durham & Melville, 1957

DIAGNOSIS. Irregular echinoids with meridosternous or orthosternous plastron, paired ambulacra flush on test; apical disc elongate with one or both ocular plates inserted between anterior and posterior pairs of genital plates.

Family **HOLASTERIDAE** Pictet, 1857

Genus ***OFFASTER*** L. Agassiz, 1836

DIAGNOSIS. Small holasteroids with flat to slightly convex base and vaulted upper surface. Apical disc with four gonopores. Frontal groove absent aborally, slightly depressed at ambitus and subambitally, at least in small individuals. Peristome oval to D-shaped; facing downwards, with little or no labral projection. Plastron meridosternous with first two to three plates uniserially arranged. Periproct on posterior face. Marginal fasciole present, at least in juvenile stages; possibly absent in larger individuals.

Offaster leymeriei Cotteau, 1887

Pl. 4, figs 10–13; Figs 14, 15

1887b *Offaster Leymeriei* Cotteau: 661, pl. 19, figs 14, 15, pl. 20, figs 1–3.
?1927 *Offaster dallonii* Lambert: 43, pl. 3, figs 12–15.
1992 *Offaster dallonii* Gallemí: 257, photo 14.
1996 *Offaster dallonii* Wilmsen *et al.*: fig. 7.

DIAGNOSIS. Test up to 30 mm in length; width *ca.* 80–85% length; height *ca.* 65% of length. Ovate in outline; specimens larger than about 15 mm with convex anterior, smaller individuals with slight anterior sulcus developed from ambitus adorally. Peristome moderately large, oval, 15% test length from the anterior. Periproct large, occupying the upper part of the posterior face, which slopes very slightly inwards so that the periproct is just visible from below but not from above. Plastron plating meridosternous. Tuberculation relatively fine, with no primaries differentiated aborally. Small individuals show a clear marginal fasciole around the posterior margin of the test; this fasciole may be lost in large individuals.

OCCURRENCE. Maastrichtian, horizons 3 and 5, Santander. Maastrichtian, horizons 5 and 6, Olazagutia Pass, Navarra. Lower Maastrichtian, Homes Morts Member, Salàs de Pallars, Tremp Basin (Gallemí, 1992). The type comes from the Upper Cretaceous (?Maastrichtian) of Roquefort, Haute-Garonne, France.

MATERIAL STUDIED. BMNH EE6170–72, EE6263–64, MGB 37459, 37543, 37548–49.

REMARKS. This species was originally placed in *Offaster* by Cotteau (1887b) and Lambert (1927), but differs from the type species of that genus, *O. pilula* (Lamarck), in lacking a clear marginal fasciole, as originally pointed out by Lambert when setting up this species. *O. pilula* and *O. leymeriei* both have rather rudimentary aboral pores and have almost no anterior sulcus. We have found that small individuals (<15 mm) have a clearly developed marginal fasciole and that this is largely lost during growth. These small individuals also have a slight anterior sulcus developed from the ambitus adorally, like *O. pilula*.

Cotteau (1887b) erected the species *Offaster leymeriei* on the basis of a 30 mm individual from the Upper Cretaceous (?Maastrichtian) of Roquefort, Haute-Garonne, France. Lambert (1927) subsequently erected the species *O. dallonii* from the Maastrichtian of Sapeira, near Tremp, Catalonia. Lambert compared his species with Cotteau's and separated *dallonii* on the grounds that it was smaller, a little less elongate, its lower face less flat, its peristome more anterior and opening not within a depression, but slightly raised, its periproct is slightly higher and its ambulacral plates are less tall and the pore-pairs are more closely spaced. We have not been able to study Cotteau's type material, but suspect that the differences cited by Lambert are more apparent than real and derive largely from the artistic rendition of the specimens in question. In any case, topotype material of *O. leymeriei* from Roquefort (BMNH E9465) is indistinguishable from our material from both Tremp and Santander.

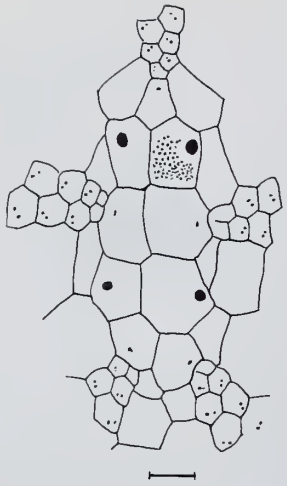

Fig. 14 Camera lucida drawing of plating in *Offaster leymeriei* Cotteau, 1887 from the Maastrichtian of the coast west of Cabo Mayor (Santander, Cantabria); MGB 37549, apical disc. Scale bar = 1 mm.

Genus ***CARDIASTER*** Forbes, 1850

DIAGNOSIS. Cordiform in outline. Petals distinct, though small, with asymmetric columns, the posterior columns being slightly narrower than the anterior columns. An anterior sulcus runs from apex to peristome, and is deepest at the ambitus. Plastron plating biserial after the initial two or three plates. A marginal fasciole is developed around posterior and lateral parts of the test.

Cardiaster sp. Pl. 4, fig. 19; Fig. 16

DIAGNOSIS. Test up to 40 mm in length, width about 85% of length, cordiform in outline with distinct anterior groove; tapering to a blunt point posteriorly. Upper surface with median ridge and sloping sides; disc plating not preserved in either specimen. Petals flush; columns of pore-pairs unequal, with posterior series better developed than anterior series pores. Pore-pairs not joined by conjugate groove and the two pores are angled to each other. Peristome slightly depressed, kidney-shaped. Plastron broad, with biserial plating following a triangular labral plate. Periproct posterior. Fascioles not present around the anterior margin; elsewhere, test preservation too abraded to tell. Larger aboral tubercules lie along the margins of the anterior groove and a few are also present adapically.

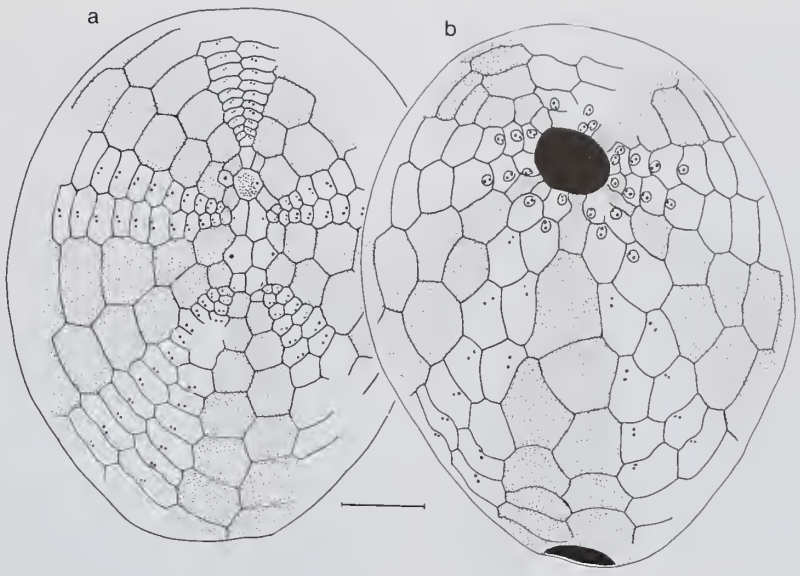

Fig. 15 Camera lucida drawing of plating in *Offaster leymeriei* Cotteau, 1887 from the Maastrichtian of the coast west of Cabo Mayor (Santander, Cantabria). BMNH EE6170. **a**, apical surface; **b**, oral surface. Interambulacra shaded. Scale bar = 5 mm.

OCCURRENCE. Upper Thanetian of Casas de Oraien, Navarra province, Spain.

MATERIAL STUDIED. BMNH EE6174–75.

REMARKS. Although both specimens are incomplete, the cordiform outline and distinctive plastron plating are indicative of just two holasteroid taxa, *Cardiaster* or *Pseudholaster*. *Cardiaster* has the labral plate and first sternal plate arranged uniserially, whereas *Pseudholaster* has the labral plate extending to touch the outer edge of the second labral plate. Furthermore, *Cardiaster* has a marginal fasciole that disappears towards the anterior, whereas *Pseudholaster* has no fascioles whatsoever. Unfortunately, preservation is so poor that the presence or absence of a marginal fasciole towards the posterior of the test cannot be confirmed. Plastron plating, however, is more decisive, in that the labral plate appears to be short and well separated from the second sternal plate. For this reason we assign the specimens to *Cardiaster*.

Our specimens differs from the common Maastrichtian *Cardiaster granulosus* (Goldfuss) in having a wider plastron with plates in each column extending less far towards the opposite ambulacrum. It also lacks enlarged primary tubercles running up the aboral surface of the anterior interambulacra, which are characteristic of *C. granulosus*.

Genus *HEMIPNEUSTES* L. Agassiz, 1836

DIAGNOSIS. Test cordate with flat base and domed upper surface. Apical disc elongate with four gonopores; madrepores typically extend over the anterior two genital plates. Paired ambulacra petaloid with petal columns strongly unequal, the posterior column of porepairs always being very much better developed. The anterior petals are flexed strongly to the anterior. Frontal groove distinct from apex to peristome, with sharp, but not keeled, margins. Periproct posterior, with test indented immediately beneath periproct so that the opening is just visible from below. Plastron composed of cuniform alternating plates that extend almost across the full width of the plastron. No fascicoles.

Hemipneustes striatoradiatus (Leske, 1778)

Pl. 7, figs 3, 4

1778 *Spatangus striato-radiatus* Leske: 104, pl. 14, fig. A.
1855 *Holaster striato-radiatus* d'Orbigny: 113, pls 802, 803.
1875 *Hemipneustes leymeriei* Hébert: 594, pl. 20.
1892 *Hemipneustes leymeriei* Hébert; Nicklès: 110.

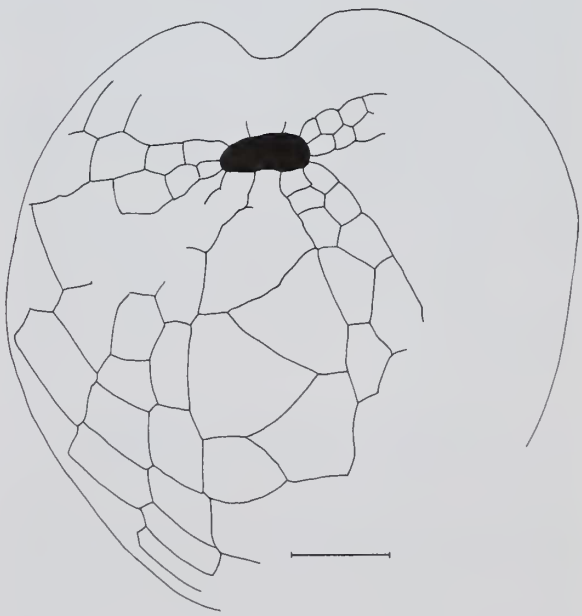

Fig. 16 Camera lucida drawing of plating in *Cardiaster* sp. from the late Thanetian of Casas de Oraien (Navarra); BMNH EE6174, oral surface. Scale bar = 5 mm.

1907 *Hemipneustes leymeriei* Hébert; Lambert: 709.
1935 *Spatangoides striatoradiatus* Leske; Smiser: 71, pl. 8, fig. 1.
1973 *Hemipneustes leymeriei* Hébert; Radig: 13.
1987 *Hemipnesutes striatoradiatus* Leske; Van der Ham *et al.*: 32, pl. 18, fig. 2.
1995 *Hemipneustes striatoradiatus* Gallemí *et al.*: table 1.

DIAGNOSIS. Test 66 mm in length; tall (height 75% of length); oval in outline and only slightly longer than wide. Upper surface strongly domed in both lateral and posterior profiles. Anterior sulcus narrow and sharply defined at the ambitus.

OCCURRENCE. Maastrichtian, horizon 4, Olazagutia Pass, Navarra province. ?Maastrichtian, horizon 2, Santander.

MATERIAL STUDIED. BMNH EE6179, MGB 37442–43.

REMARKS. Only three specimens of this species were found along with the very much more common *H. pyrenaicus* Hébert at Olazagutia Pass. They are easily distinguished from that species by their domed profile and very much more circular outline.

Fragments of a rather tall, domal *Hemipneustes* are found in the lower beds at Santander. Unfortunately, these are too incomplete to be certain of their specific identity.

Hemipneustes pyrenaicus Hébert, 1875 Pl. 7, figs 1, 2

1875 *Hemipneustes pyrenaicus* Hébert: 593, pl. 19.
1892 *Hemipneusts arnaudi* Cotteau: 165, pl. 21, figs 3, 4.
1892 *Hemipneustes pyrenaicus* Hébert; Nicklès: 110.
1907 *Hemipneustes pyrenaicus* Hébert; Lambert: 709.
1920 *Hemipneustes pyrenaicus* Hébert; Lambert: 25.
1973 *Hemipneustes pyrenaicus* Hébert; Radig: 57, pl. 8, figs 6–9, pl. 9, figs 1–4.
1992 *Hemipneustes pyrenaicus* Hébert; Gallemí: 244, photo 13.
?1996 *Hemipneustes pyrenaicus* Hébert; Wilmsen *et al.*: 354.

DIAGNOSIS. Test up to 95 mm in length; elongate, with width 75–80% of length; height 60–65% of length; subquadrate in profile with slight peak centrally. Ambulacral groove narrow; apical disc central to a little anterior. Periproct opening on inward-sloping portion of test and thus just visible in oral view.

OCCURRENCE. Maastrichtian, beds 2–4, Olazagutia Pass, Navarra province; Maastrichtian, Somo Beach near Santander, Cantabria province; Lower Maastrichtian, Homes Morts Member, Salàs de Pallars, Tremp Basin, Catalonia (Gallemí 1977).

MATERIAL STUDIED. BMNH EE4381, EE6180–87, MGB 37472, 37474–75, 37477.

REMARKS. Readily distinguished from *H. striatoradiatus* by its more elongate form, more inwardly sloping posterior face and more depressed profile.

Hemipneustes sp.

1992 *Hemipneustes leymerei* Gallemí: 240, photo 12.

DIAGNOSIS. Test longer than 80 mm (damaged at rear, but probably approximately 90 mm); rounded, almost circular with width very probably representing 90–95% of length; height around 55% of length; subrectangular in profile with a slight depression centrally where the apical system lies. Ambulacral groove narrow at the ambitus and expanding moderately towards the frontal part of the apical surface. Periproct unknown.

OCCURRENCE. Maastrichtian, horizon 4, Santander. Homes Morts Member, Lower Maastrichtian, Salàs de Pallars, Tremp Basin (Gallemí, 1992).

MATERIAL STUDIED. MGB 37533.

REMARKS. Distinguished from *H. pyrenaicus* and *H. striatoradiatus* by its rounded, almost circular form and from the latter species also by its more depressed, flat-topped profile.

Family **ECHINOCORIDAE** Lambert, 1917

Genus *ECHINOCORYS* Leske, 1778

DIAGNOSIS. Test hemispherical to subconical with flat base; no frontal groove. Apical disc central; holasterid in form with four gonopores; madrepores confined to genital plate 2. Peristome D-shaped and downward facing; test generally slightly depressed towards opening. All ambulacra similar, non-petaloid; pore-pairs small and double aborally. Periproct transverse; on lower surface. Plastron meridosternous. No fascioles.

REMARKS. *Echinocorys* has been divided into a large number of species on the basis of overall shape. Although individual morphologies can be very distinctive and of great use for local correlation, there is also a great deal of integradation amongst forms, with similar extremes of shape recurring at different times in the history of the group. As there are no structural differences in the form of the test, we here assign all forms to one large species complex, *E. scutata* Leske, and recognize the various shape varieties as named forms.

Echinocorys scutata Leske, 1778

1778 *Echinocorys scutata* Leske: 111, pl. 15, figs a, b.

DIAGNOSIS. Ambulacral plates becoming low and densely packed adapically; aboral pore-pairs small and circumflexed, becoming denser adapically, but not conjugate and not forming distinct petals.

Echinocorys scutata forma *ovata* Leske, 1778 Fig. 17a

1778 *Echinocorytes ovatus* Leske: 178, pl. 53, fig. 3.
1801 *Anachytes ovatus* Lamarck: 347.
1903 *Echinocorys ovatus* Leske; Lambert: 69, pl. 4, figs 6, 7, pl. 5, figs 1, 2.

DIAGNOSIS. Test up to 90 mm in length and ovate in outline; width approximately 75–85% of length. Subconical in profile, varying from flat-topped to distinctly pointed. Height 67–80% of length. Ambitus low and a little depressed towards the peristome. Aboral pore-pairs small and circumflexed; becoming more crowded adapically, but not forming distinct petals and never conjugate.

OCCURRENCE. Maastrichtian, horizon 3, Santander, Cantabria; Lower Maastrichtian, black-shale facies, Sarasate, motorway section, Navarra.

MATERIAL STUDIED. BMNH EE4567, BMUW 94788, 95005, 95006, 95014, 94780, 94787, 94786, 95012–13, 94783, 94788, 94996–98, 94791.

Echinocorys scutata forma *belgica* Lambert, 1898 Fig. 17b

1829 *Anachytes sulcatus* Goldfuss: 146 (pars), pl. 45, fig. 1a–c only.
1898b *Echinocorys belgicus* Lambert: 43, pl. 4, figs 9, 10.
1903 *Echinocorys belgicus* Lambert; Lambert: 80.
1996 *Echinocorys belgicus* Lambert; Wilmsen *et al.*: 354.

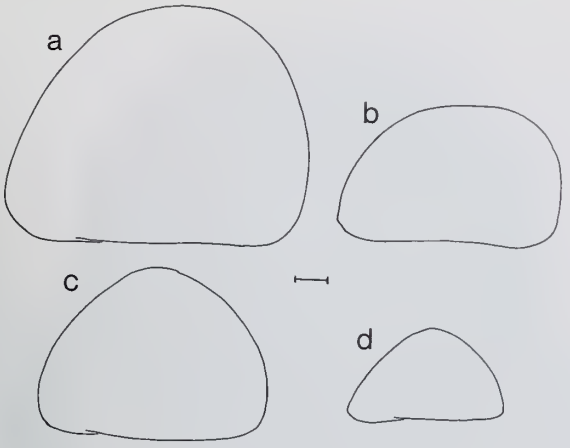

Fig. 17 Outlines of tests of *Echinocorys scutata* Leske in lateral profile (anterior to the right). **a**, forma *ovata* Leske, 1778, BMNH EE6194, Maastrichtian of Santander, Cantabria. **b**, forma *belgica* Lambert, 1898, BMNH EE6193, Maastrichtian of Santander. **c**, forma *cotteaui* Lambert, 1903, BMNH EE6191, Late Thanetian of Casas de Oraien, Navarra. **d**, forma *pyrenaica* Seunes, 1888, BMNH EE6192, Danian of Erice, Navarra.

DIAGNOSIS. Test 62 mm in length and 58 mm in width (width 94% of length); ovate, with rounded anterior and slightly pointed posterior. Height 35 mm (56% of length); with broad, rather flat, upper surface, steeply sloping anterior and more gently sloping posterior. Ambitus very low. Lower surface distinctly sunken inside margins. Petals small and non-conjugate; becoming denser towards apex.

OCCURRENCE. Maastrichtian, level 5, Santander.

MATERIAL STUDIED. BMNH EE6194.

REMARKS. Distinguished from other forms by its wide, subcircular outline and depressed lateral profile.

Echinocorys scutata forma *pyrenaica* Seunes, 1888

Fig. 17d

1888a *Echinocorys pyrenaicus* Seunes: 814, pl. 30, fig. 5, pl. 31, fig. 2.
1927 *Echinocorys obliquus* [Nilsson MS] Ravn: 336, pl. 4, fig. 2, pl. 5, fig. 2.

DIAGNOSIS. Small form up to 50 mm in length; width 85–90% of length; ovate and slightly pointed posteriorly. Flat base with sharp and low ambitus. Upper surface conical in lateral and posterior profile; height approximately 50% of test length. Periproct on oral surface. Aboral pore-pairs small; becoming more closely-spaced adapically.

OCCURRENCE. Danian *Coraster* Beds, Erice, Navarra. Also known from the Danian of Alfàs del Pi, Alicante, Spain. The type of *obliquus* comes from the Upper Danian of Denmark.

MATERIAL STUDIED. BMNH EE6192, MGB 37323.

REMARKS. The strongly conical profile and sharp ambitus distinguish this form from all others.

Echinocorys scutata forma *cotteaui* Lambert, 1903

Pl. 4, figs 20–22, Pl. 7, figs 5, 6; Fig. 17c

1847 *Ananchytes semiglobus* Goldfuss; Agassiz & Desor: 136 (*pars*).
1856 *Echinocorys vulgaris* Breynius; Leymerie & Cotteau: 343.
1877 *Echinocorys semiglobus* Goldfuss; Cotteau: 62, pl. 5, figs 14–18.
1887b *Echinocorys semiglobus* Goldfuss; Cotteau: 662.
1890 *Echinocorys semiglobus* Goldfuss; Seunes: 194.
1903 *Echinocorys cotteaui* Lambert: 84, pl. 4, fig. 8.
1907 *Echinocorys cotteaui* Lambert; Lambert: 718.

DIAGNOSIS. Test small, up to 70 mm length only; width 85–95% test length, ovate in outline. Test low conical in profile, height 65–73% of test length. Ambulacra simple and identical, with pore-pairs becoming moderately dense towards the apex, but remaining small and semi-colon-like; no clearly defined petaloid area. Peristome slightly wider and perioral area more depressed, forming characteristic rounded anterior rim.

OCCURRENCE. Upper Thanetian. Casas de Oraien, Navarra province, Spain.

MATERIAL STUDIED. BMNH EE4530–4534, EE6189–91, MGB 37403–37405, 37429–37432.

REMARKS. Differs from forma *belgica* in profile; that form being very much more flat topped. Less conical and with a more rounded ambitus than forma *pyrenaica*.

Genus *JERONIA* Seunes, 1888

DIAGNOSIS. Ovate in outline with domed upper surface and flat base; distinctly pointed at posterior. Apical disc holasterid, with three gonopores (genital plate 2 without a gonopore). Aboral pore-pairs small and insignificant, placed centrally towards lower edge of ambulacral plates and not crowded or enlarged adapically. Peristome ovate and downward-facing; rather strongly depressed; oval. Periproct inframarginal, opening on posterior projection. Tuberculation generally fine, but with prominent band of very large primary tubercles around the ambitus. Plastron plating meridosternous; very narrow.

REMARKS. Similar to *Echinocorys* in shape, but with a stronger sternal keel and distinct posterior point, and with a supra-ambital band of large tubercles around the posterior of the test.

Jeronia pyrenaica Seunes, 1888

Figs 18–20

1888a *Jeronia pyrenaica* Seunes: 810, text-figs 1–3, pl. 30, fig. 1.
?1889 *Offaster cuneatus* Seunes: 806, pl. 24, fig. 3.
1891 *Jeronia pyrenaica* Seunes: 29, text-figs 4, 5, pl. 3, figs 1, 2.
1975 *Jeronia pyrenaica* Seunes; Plaziat *et al.*: 634, fig. 10.

DIAGNOSIS. As for genus. In both specimens which show the apical disc plating genital plate 2 has only madrepores and no gonopore, as first illustrated by Seunes (1891).

OCCURRENCE. Near base of chalk facies; Upper Danian, Larumbe; basal Thanetian, *G. angulata* Zone (ZB 5), Aristregui, Navarra province.

MATERIAL STUDIED. BMNH EE6195, MGB 37353, 37382–37383.

Fig. 18 *Jeronia pyrenaica* Seunes, 1888, from the late Danian of Larumbe (Navarra); MGB 37382, **1**, apical surface; **2**, oral surface; **3**, posterior profile; **4**, lateral profile. All ×1.5.

Family **STEGASTERIDAE** Lambert, 1917

DIAGNOSIS. Test cordate, with prominent frontal groove from the ambitus to the peristome. Apical disc holasterid with four gonopores. Paired ambulacra with subpetaloid to rudimentary pore-pairs. Phyllode pore-pairs lacking from around peristome. Plastron orthosternous without rostral plate. Marginal fasciole may be present, but no other fascioles are developed.

Genus ***STEGASTER*** Pomel, 1883

DIAGNOSIS. Thick-tested holasterid with flat base and cordate outline. Frontal groove absent adapically, deepening to ambitus with sharp keels and continuing as well-defined furrow to mouth. Petals rudimentary, flush. Plastron orthosternous. Periproct on posterior face, just supramarginal with subanal tallon. No fascioles.

Stegaster bouillei (Cotteau, *in* de Bouillé, 1873)

Pl. 5, figs 1–3; Figs 21, 22

1873 *Holaster Bouillei* Cotteau, *in* de Bouillé: 450.
1889 *Stegaster bouillei* Seunes: 816, pl. 26, fig. 2.
1892 *Stegaster bouillei* Nicklès: 111.

DIAGNOSIS. Test elongate, up to 75 mm in length; tapering to posterior truncation. Width about 90% of length. In profile subconical with tallest point anterior; height about 50–60% of length. Anterior

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PLATE 5

Figs 1–3 *Stegaster bouillei* (Cotteau, *in* de Bouillè, 1873), BMNH EE6066, Maastrichtian of Sarasate, Navarra. Oral, apical and lateral views, ×1.

Figs 4–6 *Stegaster palaeocenicus* sp. nov., MGB 37351 (**holotype**), Danian of Aristregui, Navarra. Lateral, oral and aboral views, ×1.


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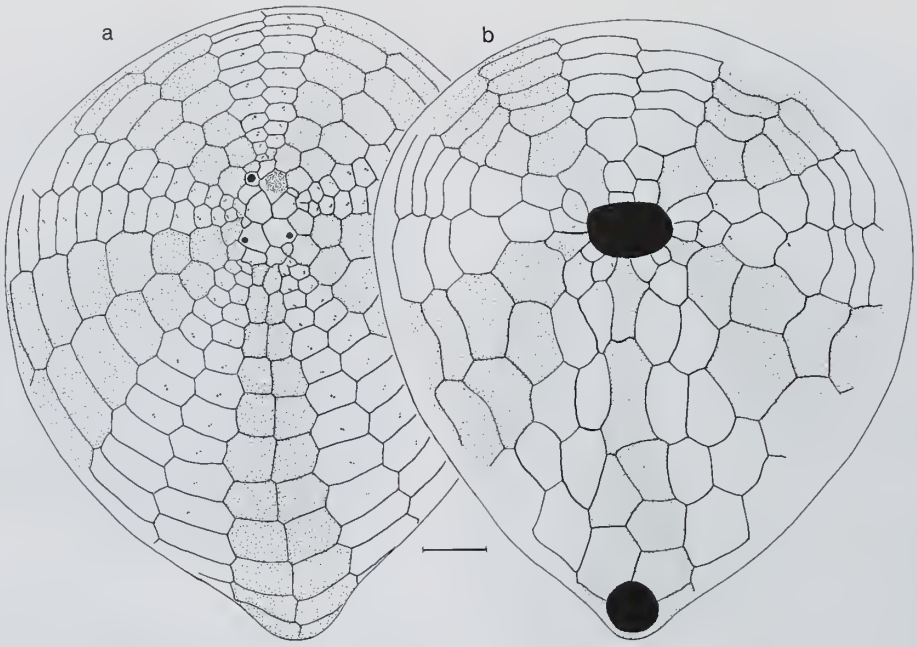


Fig. 19 Camera lucida drawings of plating in *Jeronia pyrenaica* Seunes, 1888, from the late Danian of Larumbe (Navarra); MGB 37382, **a**, apical surface; **b**, oral surface. Interambulacra shaded. Scale bar = 5 mm.

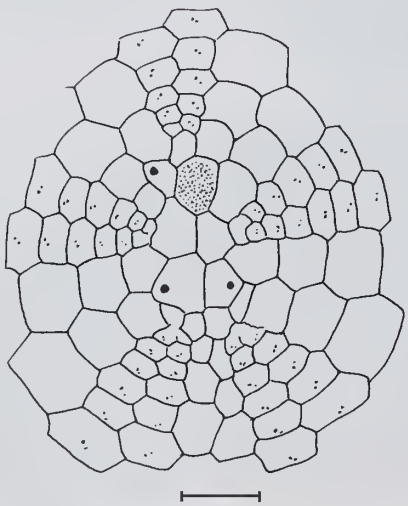


Fig. 20 Camera lucida drawing of plating in *Jeronia pyrenaica* Seunes, 1888 from the late Danian of Aristregui (Navarra); MGB 37353, apical disc. Scale bar = 5 mm.

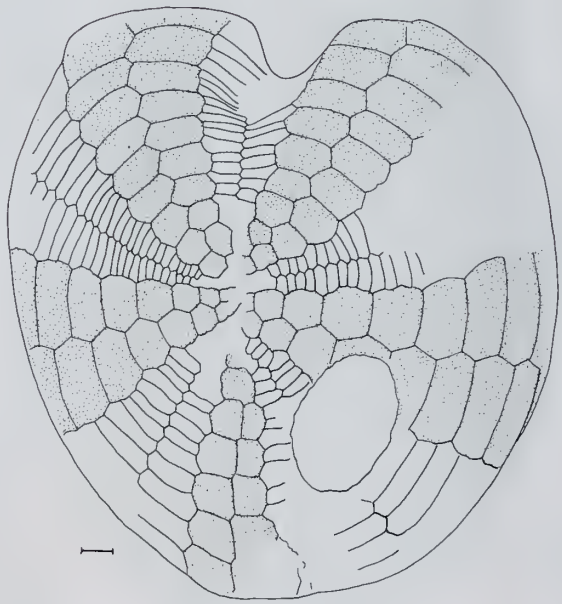


Fig. 21 Camera lucida drawing of plating in *Stegaster bouillei* (Cotteau, *in* de Bouillé, 1873) from the late Maastrichtian of Bidart (Pyrénées-Atlantiques, France); BMUW 74753, apical surface (interambulacra shaded). Scale bar = 5 mm.

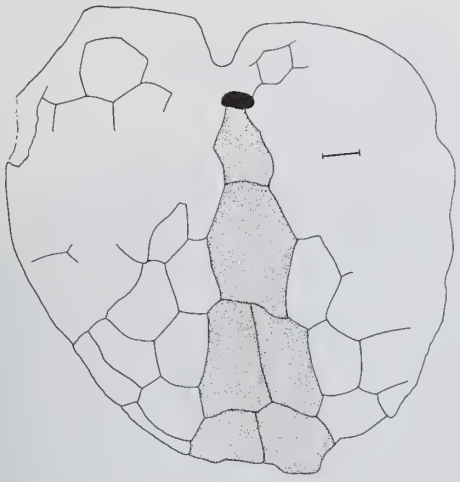


Fig. 22 Camera lucida drawing of plating in *Stegaster bouillei* (Cotteau, *in* de Bouillé, 1873) from the late Maastrichtian of Bidart (Pyrenées-Atlantiques, France); BMUW 94988, oral surface (interambulacra shaded). Scale bar = 5 mm.

sulcus sharp and well developed, forming obvious narrow groove on oral surface. Ambulacral plates low and relatively wide, compared to *S. altus*, and with elongate pore-pairs en chevron. Larger primary tubercles present close to the apex and along the posterior ridge between the apex and periproct. Larger tubercles also developed just above the ambitus around the posterior part of the test. Periproct supra-ambital, but test depressed below the periproct so that the periproct opening is just visible in oral view.

OCCURRENCE. Lower Maastrichtian (black shale facies), Sarasate, Navarra; upper Upper Maastrichtian, Bidart, Pyrenées-Atlantiques, France. The species was first described from the Maastrichtian of the French Pyrenees between Gan and Rébénac, and is also known from the Province of Alicante, Spain and from Turkey, Crimean peninsula, Republic of Georgia, and the North Caucasus.

MATERIAL STUDIED. BMNH EE4375, EE4568, EE4566, EE6066, MGB 37286–87, 37300.

REMARKS. Easily separated from *S. altus* by its characteristic elongate shape and vaulted upper surface with the tallest point anterior. *S. cotteaui* differs in having a disjunct plastron and a more ovate outline.

Stegaster altus Seunes, 1889

1889 *Stegaster altus* Seunes: 815, pl. 26, fig. 1.
1891 *Stegaster chalmasi* Seunes: 23, pl. 1, fig. 1.
1892 *Stegaster chalmasi* Seunes; Nicklès: 110.
1892 *Stegaster altus* Seunes; Nicklès: 111.
1995 *Stegaster novoi* Lambert; Gallemí *et al.*: 269, table 1.

DIAGNOSIS. Test up to 50 mm in length. Like *S. boullei,* but test almost as wide as long and very tall; height more than 70% of test length. Ambulacral plates much taller than in *S. bouillei.*

OCCURRENCE. Lower Maastrichtian (black shale facies), Sarasate, Navarra. Upper Upper Maastrichtian, Bidart, Pyrenées-Atlantiques, France. This species was first described from the Maastrichtian of the French Pyrenees. It also occurs in the Alicante Province of Spain and in Tunisia, Turkey, Bulgaria, Republic of Georgia and the North Caucasus.

MATERIAL STUDIED. BMNH EE4396, EE4347–50, EE6176–78, MGB 37298–99, BMUW 74610, 74753, 74788, 74945, 94946, 94949, 94988, 94994.

REMARKS. Readily distinguished from other species of *Stegaster* by its wider and much taller test.

Stegaster cotteaui Seunes, 1889

Pl. 6, figs 1–5; Figs 23, 24

1889 *Stegaster cotteaui* Seunes: 813, pl. 25, fig. 3.

DIAGNOSIS. Test up to 60 mm in diameter; cordiform, as wide as long or slightly wider. All material crushed, but apparently rather rounded at the ambitus when not crushed and not very tall; tallest point anterior of mid-length. Ambulacral plates rather tall with small, almost rudimentary pore-pairs. Plastron disjunct with labral plate separated from succeeding sternal plate by ambulacral plates. Tuberculation unknown.

OCCURRENCE. Upper Upper Maastrichtian, Bidart, Pyrenées-Atlantiques, France.

MATERIAL STUDIED. BMNH 75697, E2916, E10972, BMUW 74603, 74607, 74609a, 74772, 74789, 74791, 94946, 94948, 94985, 94986, 94989, 94991a.

REMARKS. Most similar to *Stegaster heberti*, differing primarily in having a disjunct plastron (a feature which we can confirm is not size-related). It comes very close to *Sanchezaster habanensis* Lambert in appearance, differing only in having double pores on ambulacral plates rather than single pores.

Stegaster palaeocenicus Smith & Gallemí, sp. nov.

Pl. 5, figs 4–6; Fig. 25

DIAGNOSIS. *Stegaster* with disjunct plastron and posterio-lateral interambulacra.

DESCRIPTION. Test up to 55 mm in length; ovate with slight anterior invagination and small bilobed posterior projection in aboral plan view. Distinctly conical in profile with tallest point coincident with apical disc; rounded in front and sloping to rear. Frontal groove absent adapically, but rapidly deepening at the ambitus and continuing as a deep channel to the peristome, which is forward-facing. The interambulacral plates on either side form a distinct keel. Apical disc positioned anteriorly (about 30% test length from the anterior border); elongate and of standard holasterid structure with four gonopores. Aboral pore-pairs small and sunken; never elongate; becoming microscopic away from the apical disc. Plastron orthosternous and disjunct, with ambulacral plates separating the labrum and first sternal plate. The latero-posterior interambulacra are also disjunct. Periproct supra-ambital, on short posterior face and above small double protuberance. Aboral tuberculation composed of a uniform scattering of small tubercles set in a dense granulation; no enlarged tubercles differentiated. No marginal fasciole.

OCCURRENCE. Late Danian of Aristregui and Larumbe, Navarra Province.

TYPES. Holotype MGB 37351, paratypes MGB37352, 37381.

REMARKS. The deep sulcus developed from the ambitus to the peristome identifies this as a stegasterid. Our species lacks the marginal fasciole and enlarged tubercles of *Guettaria* and *Rispolia*,

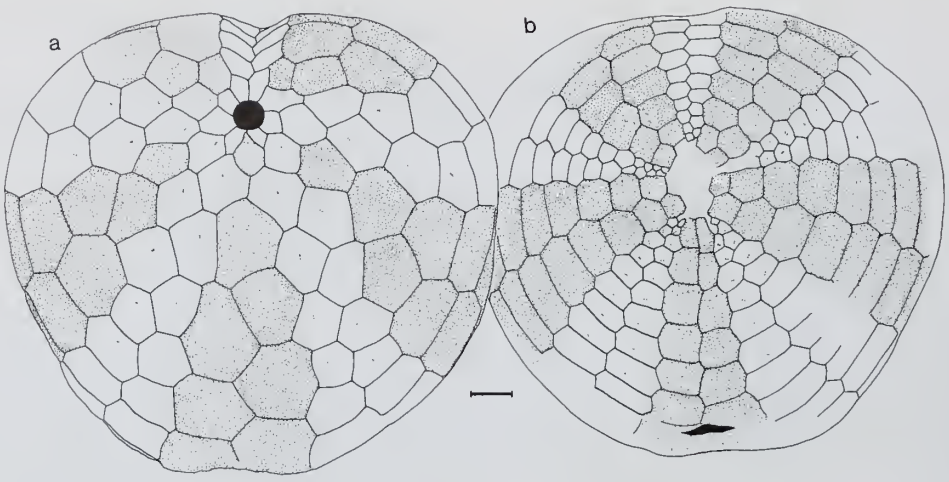


Fig. 23 Camera lucida drawings of plating in *Stegaster cotteaui* Seunes, 1889, from the late Maastrichtian of Bidart (Pyrénées-Atlantiques, France); BMUW 74603, **a**, oral surface; **b**, apical surface (interambulacra shaded). Scale bar = 5 mm.

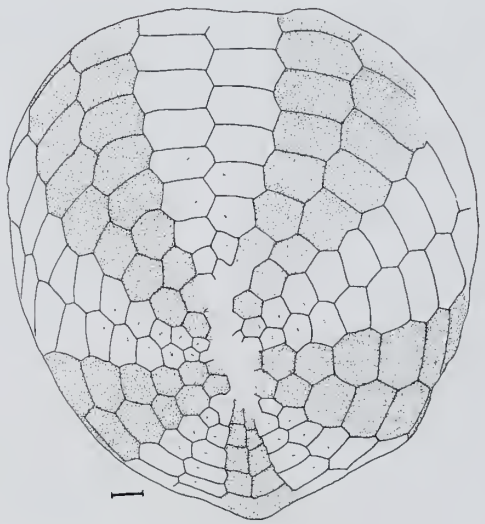


Fig. 24 Camera lucida drawing of plating in *Stegaster cotteaui* Seunes, 1889, from the late Maastrichtian of Bidart (Pyrénées-Atlantiques, France); BMUW 74792, apical surface (interambulacra shaded). Scale bar = 5 mm.

and its disjunct plastron distinguishes it from all but three species of *Stegaster*, *S. cotteaui* Seunes, *S. charlesi* Lambert and *S. mairei* Lambert, all Maastrichtian in age. In none of these are the latero-posterior interambulacra interupted as they are in our species. *S. mairei* further differs in being subglobular in shape with its periproct positioned much higher. *S. cotteaui* has a much narrower anterior sulcus, more anterior peristome (10% test length from the anterior rather than almost 30%) and is more depressed in profile. *S. charlesi* resembles our species in profile, but, according to Lambert (1931: M7), has such a reduced labral plate that only ambulacral plates surrounding the peristome. Unfortunately the only plating diagram of *S. charlesi* (Lambert 1931: M5, fig. 3) gives insufficient detail and we have not examined Lambert's type to confirm this very unusual plate arrangement.

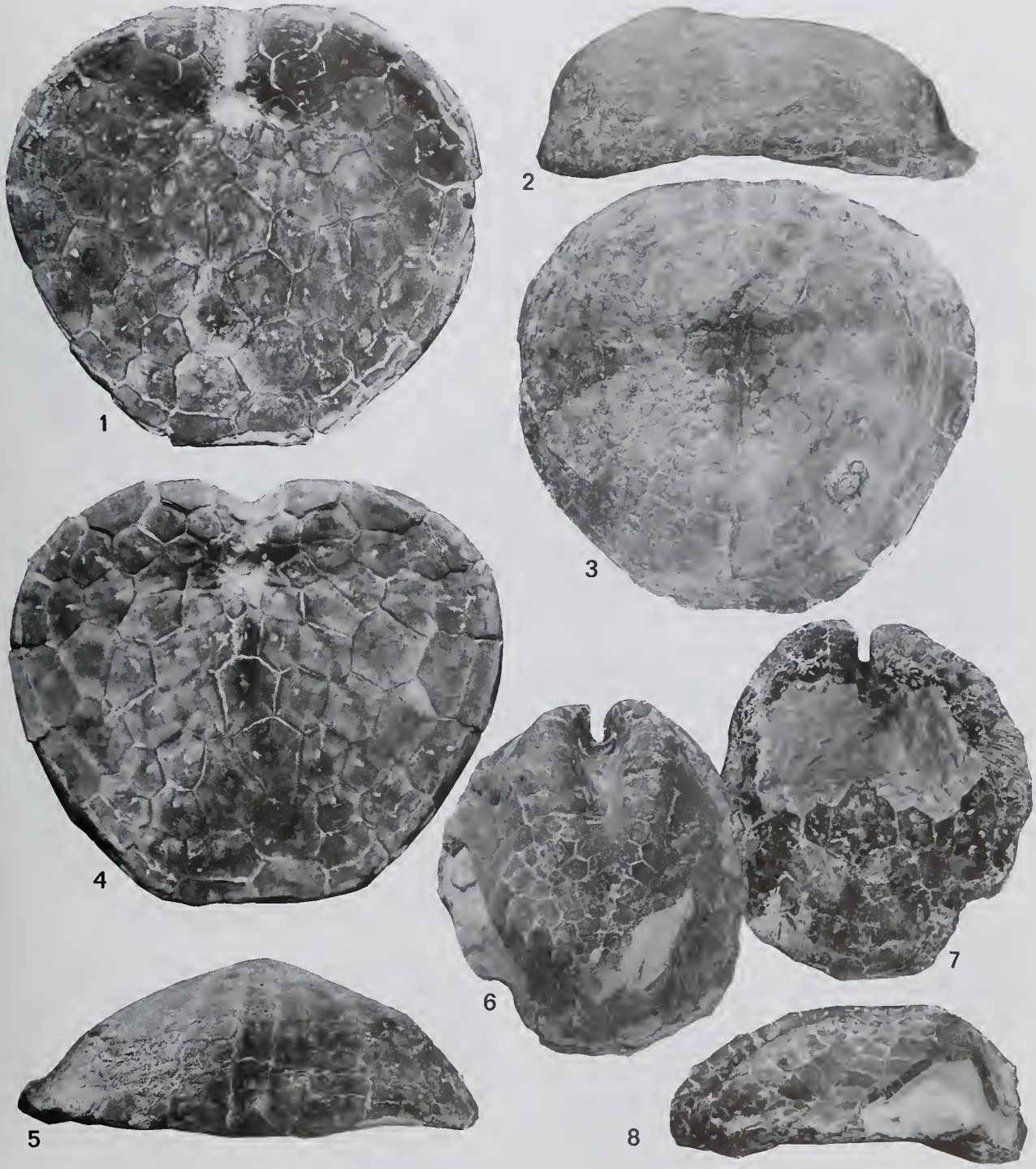
Genus ***THOLASTER*** Seunes, 1891

DIAGNOSIS. Test elongate with very deep frontal groove at ambitus and adorally; tapering to posterior truncation. Apical disc with four genital plates each with a gonopore. Aboral pore-pairs rudimentary, ambulacra flush. Frontal groove with sharp lateral carina; developed from apex to peristome. Oral surface flat. Plastron orthosternous. Periproct on posterior face. Very large primary tubercles prominent towards apex and along the aboral margins of the frontal groove. No fascioles.

PLATE 6

Figs 1–5 *Stegaster cotteaui* Seunes, 1889, Upper Maastrichtian of Bidart, Pyrenées-Atlantiques, France. **1–3**, BMUW 74603, oral, lateral and apical views, ×1. **4**, **5**, BMUW 94985, oral and lateral views, ×1.

Figs 6–8 *Tholaster munieri* (Seunes, 1889), BMUW 94993, Upper Maastrichtian of Bidart, Pyrenées-Atlantiques, France. Apical, oral and lateral views, ×1.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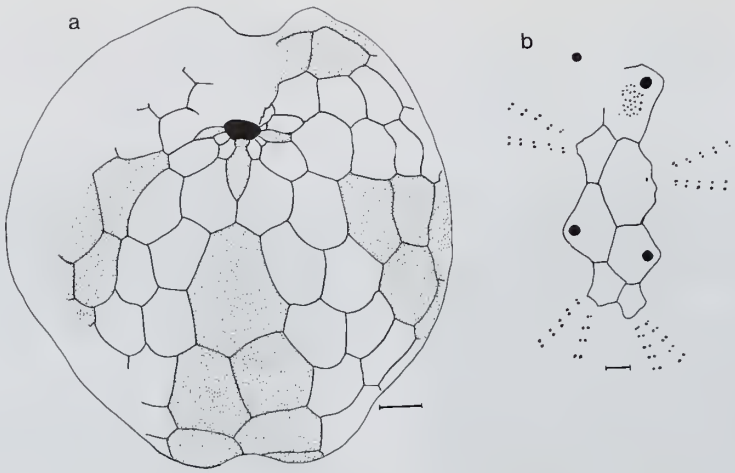

Fig. 25 Camera lucida drawings of plating in *Stegaster palaeocenicus* sp. nov. from the late Danian of Aristregui (Navarra); **a**, holotype MGB 37351, oral surface (interambulacra shaded); **b**, paratype MGB 37352, apical disc. Scale bars: a = 5 mm; b = 1 mm.

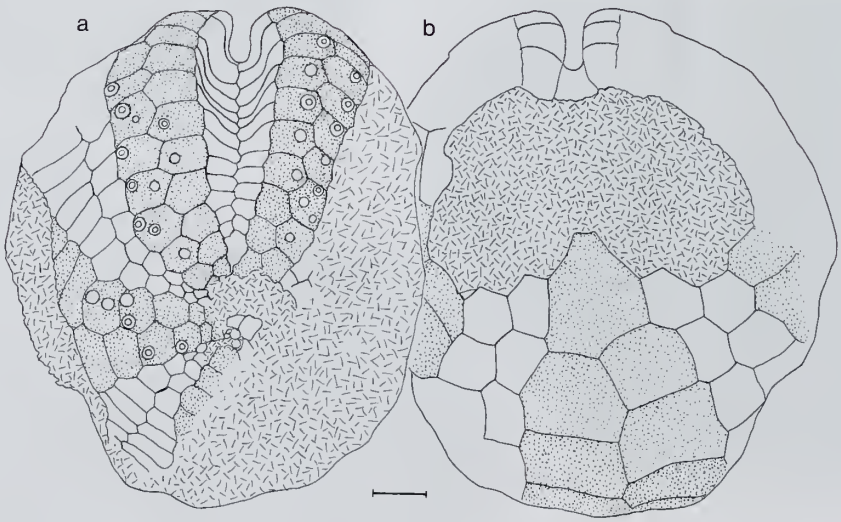

Fig. 26 Camera lucida drawings of plating in *Tholaster munieri* (Seunes, 1889) from the late Late Maastrichtian of Bidart (Pyrénées-Atlantiques, France); BMUW 94993, **a**, apical surface; **b**, oral surface. Interambulacra shaded. Scale bar = 5 mm.

PLATE 7

Figs 1, 2 *Hemipneustes pyrenaicus* Hébert, 1875, BMNH EE6180, Maastrichtian of Olazagutia Pass, Navarra. Apical and lateral views, ×1.
Figs 3, 4 *Hemipneustes striatoradiatus* (Leske, 1778), BMNH EE6179, Maastrichtian of Olazagutia Pass, Navarra. Apical and lateral views, ×1.
Figs 5, 6 *Echinocorys scutata* forma *cotteaui* Lambert, 1903, BMNH EE6190, Thanetian of Casas de Oraien, Navarra. Lateral and apical views, ×1.
Figs 7–10 *Pseudoffaster caucasicus* (Dru, 1884), BMNH EE6234, Maastrichtian of Sarasate, Navarra. Apical, posterior, lateral and oral views, ×2.


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Tholaster munieri (Seunes, 1889)
Pl. 6, figs 6–8; Fig. 26

1889 *Gibbaster munieri* Seunes: 819, pl. 27, fig. 1.
1891 *Tholaster munieri* Seunes: 23.

DIAGNOSIS. As for genus. Test up to 45 mm in length; slightly longer than wide. Both specimens crushed and height unknown.

OCCURRENCE. Upper Upper Maastrichtian, Bidart, Pyrenées-Atlantiques, France. The type comes from the Maastrichtian of the same region (Lasseube) and it has been recorded from several other localities in the Department of Landes, France.

MATERIAL STUDIED. BMUW 74768, 94993.

REMARKS. The long, deep frontal groove and prominent primary tubercles make this a very easily recognizable species.

Genus ***PSEUDOFFASTER*** Lambert, *in* Lambert & Thiéry, 1924

DIAGNOSIS. Test ovate with anterior sulcus present only below the ambitus. Ambulacra composed of tall plates with rudimentary pores. Apical disc holasterid, with four gonopores. Periproct high on steep posterior face. Peristome small, facing forwards and opening into anterior sulcus. Marginal fasciole present.

Pseudoffaster caucasicus (Dru, 1884) Pl. 7, figs 7–10; Fig. 27

1884 *Offaster caucasicus* Dru: 514, pl. 26, figs 5–10.
1927 *Pseudoffaster caucasicus* (Dru); Lambert: 42.

DIAGNOSIS. As for genus. Test 20.3 mm in length, ovate in outline; width approximately 90% of length; widest approximately midlength. Height 90% of length, with strongly convex lower surface and tallest point immediately anterior of the apical disc.

OCCURRENCE. Maastrichtian of Sarasate, Navarra, Spain. Also recorded from the Lower Maastrichtian Areny Sandstone of Tremp, Catalonia, Spain, by Lambert (1927).

MATERIAL STUDIED. BMNH EE6234.

Genus ***GALEASTER*** Seunes, 1889

DIAGNOSIS. Test ovate with shallow anterior sulcus persisting to the peristome. Tall, vaulted upper surface and keeled lower surface. All ambulacra with tall plates and rudimentary pores. Apical disc holasterid, with four gonopores; anterior pair of genital plates generally fused. Periproct high on steep posterior face. Plastron orthosternous. Peristome small, facing forwards and opening into anterior sulcus. Subanal fasciole present.

Galeaster bertrandi Seunes, 1889
Pl. 4, figs 14–18; Fig. 28

1889 *Galeaster bertrandi* Seunes: 822, pl. 27, figs 2, 3.

DIAGNOSIS. Test length 11.1 mm, width 9.0 mm, height 9.4 mm. Weakly cordiform and tapering to a point posteriorly; very tall in profile with tallest point towards the posterior, sloping anteriorly and with vertically truncate posterior. Lower surface strongly convex with keeled posterior interambulacrum. Shallow anterior sulcus from a little above the ambitus to the peristome. Apical disc plating elongate, with small gonopores just apparent at this size. Ambulacral plates very tall with pore-pairs centrally placed; pores double throughout.

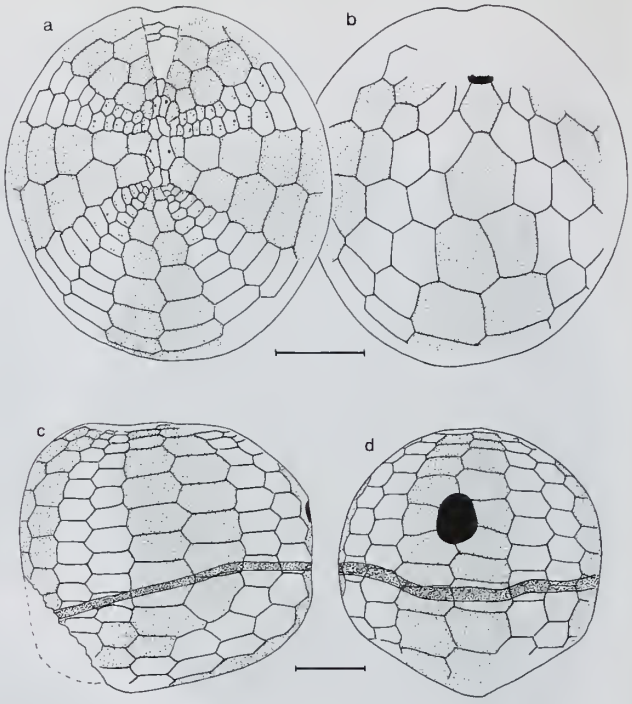


Fig. 27 Camera lucida drawings of plating in *Pseudoffaster caucasicus* (Dru, 1884) from the Maastrichtian of Sarasate (Navarra); BMNH EE6234, **a**, apical surface; **b**, oral surface; **c**, lateral profile; **d**, posterior profile. Interambulacra shaded. Scale bar = 5 mm.

OCCURRENCE. Maastrichtian, horizon 2, Santander. The type of this species was reported from the 'Garumnian' (?Maastrichtian) of the Pyrenées-Atlantiques, France.

MATERIAL STUDIED. BMNH EE6188.

REMARKS. Unfortunately, we have only a single specimen of this interesting species. The very anterior mouth, opening into the frontal groove immediately distinguishes this species from *Offaster*, whose mouth is downward-facing and not opening into an anterior sulcus. Amongst holasteroids only *Galeaster* possesses a subanal fasciole, orthosternous plating and a distinct frontal sulcus. However, the apical disc has the two anterior genital plates fused in *Galeaster*, according to Poslavskaya & Moskvin (1960), whereas our specimen undoubtedly has a suture separating genital plates two and three. We do not know what the apical disc plating in Seunes' type material is like.

Order **SPATANGOIDA** Claus, 1876

DIAGNOSIS. Ovate to heart-shaped with compact apical disc with four genital plates. Posterior interambulacral plates differentiated to form a plastron adorally. Aboral ambulacra typically with pore-pairs enlarged and forming petals; often depressed.

Family **MICRASTERIDAE** Lambert 1920

DIAGNOSIS. Apical system ethmophract; plastron mesamphisternous. Aboral tuberculation consisting of larger primary tubercles dispersed amongst a dense groundmass of fine granules.

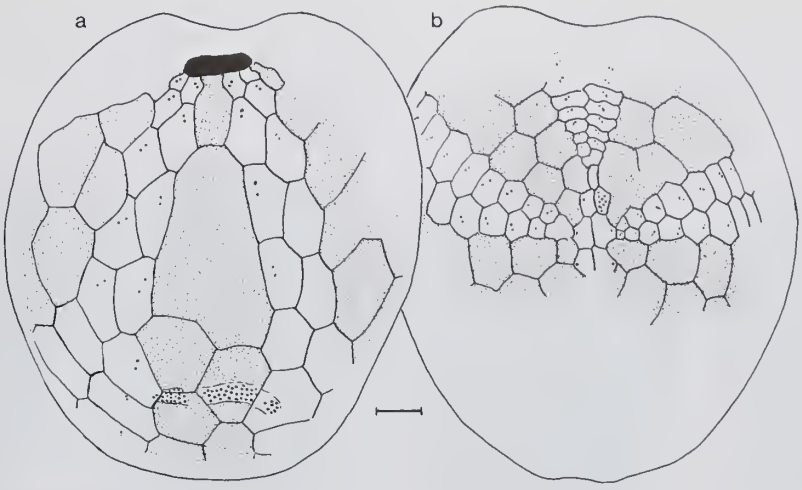


Fig. 28 Camera lucida drawings of plating in *Galeaster bertrandi* Seunes, 1889, from the Maastrichtian of the coast west of Cabo Mayor (Santander, Cantabria); BMNH EE6188, **a**, oral surface, interambulacra shaded; **b**, apical surface. Scale bar = 1 mm.

Genus ***MICRASTER*** Agassiz, 1836
Subgenus ***ISOMICRASTER*** Lambert, 1901

DIAGNOSIS. Test cordate, with shallow anterior sulcus; subconical in profile with periproct very low on short posterior face. Apical disc ethmophract with four gonopores. Anterior ambulacrum sunken with pore-pairs similar to those of other ambulacra. Peristome forward-facing and placed almost at the anterior border, largely hidden in oral view by the projecting labral plate. No subanal fasciole.

REMARKS. The forward facing peristome and strongly labiate labral plate ally this lineage with the type species, *M. coranguinum* Leske. It is distinguished, however, by its lack of a subanal fasciole and by the highly conical profile of the test.

Micraster (Isomicraster) stolleyi Lambert, 1901

1869 *Epiaster gibbus* Schlüter: 237, pl. 2, figs 1, 1a–c.
1901 *Isomicraster stolleyi* Lambert, *in* Lambert 1895a–1901a: 959.
1927 *Isomicraster dallonii* Lambert; Lambert: 48.
1975 *Micraster stolleyi* Lambert; Stokes: 79, fig. 30f.
1989 *Micraster (Isomicraster) aff. stolleyi* Lambert; Küchler & Kutz: 196, text-fig. 2.
1992 *Micraster stolleyi* Lambert; Gallemí: 335, figs 88–90.

DIAGNOSIS. As for genus. Test approximately 70 mm in length and 45 mm in height.

OCCURRENCE. ?Uppermost Campanian-?Lower Maastrichtian; Erice, Navarra, Spain.

MATERIAL STUDIED. MGB 37304.

REMARKS. This unique specimen is crushed, but cannot be mistaken for any other species. It comes from the upper beds in the shale-limestone succession immediately underlying the Danian *Coraster* Limestones at Erice. This has been determined as Upper Campanian – lowermost Maastrichtian (Küchler & Kutz, 1989).

Subgenus ***PSEUDOGIBBASTER*** Moskvin, 1983

DIAGNOSIS. Test cordate, with shallow anterior sulcus; inflated, with vertically truncated posterior. Apical disc ethmophract with four gonopores. Anterior ambulacrum sunken with pore-pairs differentiated from those of other ambulacra. Peristome almost non-labiate and downward-facing. Subanal fasciole present.

REMARKS. The non-labiate peristome differentiates this from the type species, *M. coranguinum* Leske, and from all Upper Maastrichtian species of *Micraster* from north-western Europe. It is distinguished from *Isaster* and *Cyclaster* in having four gonopores rather than three.

Micraster (Pseudogibbaster) tercensis Cotteau, 1863
Pl. 8, figs 8–12; Figs 29, 30

1856 *Micraster brevis* (Desor); Leymerie & Cotteau: 346.
1863b *Micraster cortestudinarium* Goldfuss; Cotteau: 220 (55).
1863b *Micraster tercensis* Cotteau: 221 (56).
1877 *Micraster tercensis* Cotteau; Cotteau: 69, pl. 7, figs 29–32.
1975 *Micraster tercensis* Cotteau; Plaziat *et al.*: 640, fig. 10.

DIAGNOSIS. Test up to 65 mm in length, with distinct anterior groove; tapering to a blunt point posteriorly. Width 100–110% of length. In profile, subconical with rounded base and approximately vertical posterior truncation. Apex subcentral to slightly anterior; generally a little sunken. Petals moderately long and straight; open-ended distally; anterior pair extending 70% of the radial distance to the margin, posterior pair extending only 55–65% of the distance. Petals depressed with both pores slightly elongate. Anterior ambulacrum with enlarged pores adapically (18–22 enlarged pore-pairs), forming a shallow groove to the peristome. Labral plate moderately long and narrow; sternal plates unequal, with left sternal plate having a smaller contact surface with the labral plate than the right sternal plate. Periproct small, rounded, positioned high on the posterior face. No peripetalous fasciole. Aboral tuberculation consisting of a scattering of larger primary tubercles set amongst a dense uniform groundmass of miliaries. Subanal fasciole present, enclosing four or five enlarged subanal pore-pairs.

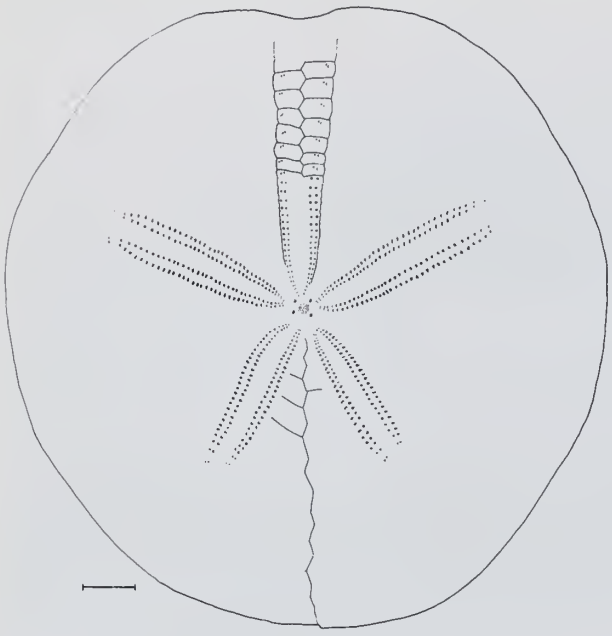


Fig. 29 Camera lucida drawing of plating in *Micraster (Pseudogibbaster) tercensis* Cotteau, 1863, from the late Thanetian of Casas de Oraien (Navarra); BMNH EE4521, apical surface. Scale bar = 5 mm.

OCCURRENCE. Upper Thanetian, *G. pseudomenardii* Zone, Casas de Oraien, Navarra province, Spain.

MATERIAL STUDIED. BMNH EE4514–21, EE6196–6201, MGB 37402, 37426–28.

Genus ***CYCLASTER*** Cotteau, *in* Leymerie & Cotteau, 1856

DIAGNOSIS. Micrasterids with three gonopores (no gonopore present on genital plate 2); commonly showing sexual dimorphism in the size of gonopores. Petals short and weakly depressed only; anterior ambulacrum with differentiated pore-pairs adapically. Peristome weakly labiate and downward-facing. Subanal fasciole present; peripetalous fasciole absent or present – when present it may be partial or complete.

Cyclaster gindrei (Seunes, 1888) Pl. 8, figs 1–5; Fig. 31b

1888a *Isopneustes gindrei* Seunes: 795, pl. 28, fig. 2.

DIAGNOSIS. Test up to 35 mm in length. Subquadrate in outline, with width 75–80% of length; widest where anterior petals reach the ambitus and tapering slightly posteriorly to a truncate posterior. Anterior margin uniformly rounded, or with feeble anterior depression in largest individuals. Petals short and well-defined; anterior pair diverging at 110–120°, posterior pair diverging at about 50° and slightly curved. Anterior and posterior petals similar in length, with 16 pore-pairs in 5 mm long petals. The posterior interambulacrum is raised as a keel aborally, and in profile forms the highest part of the test.

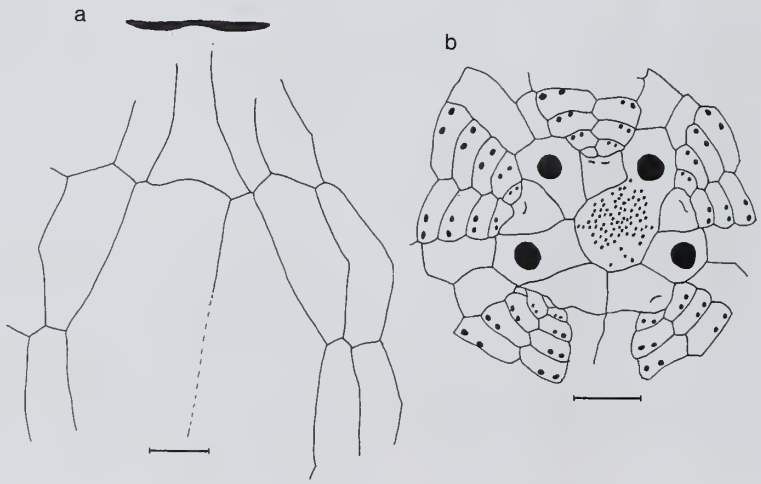


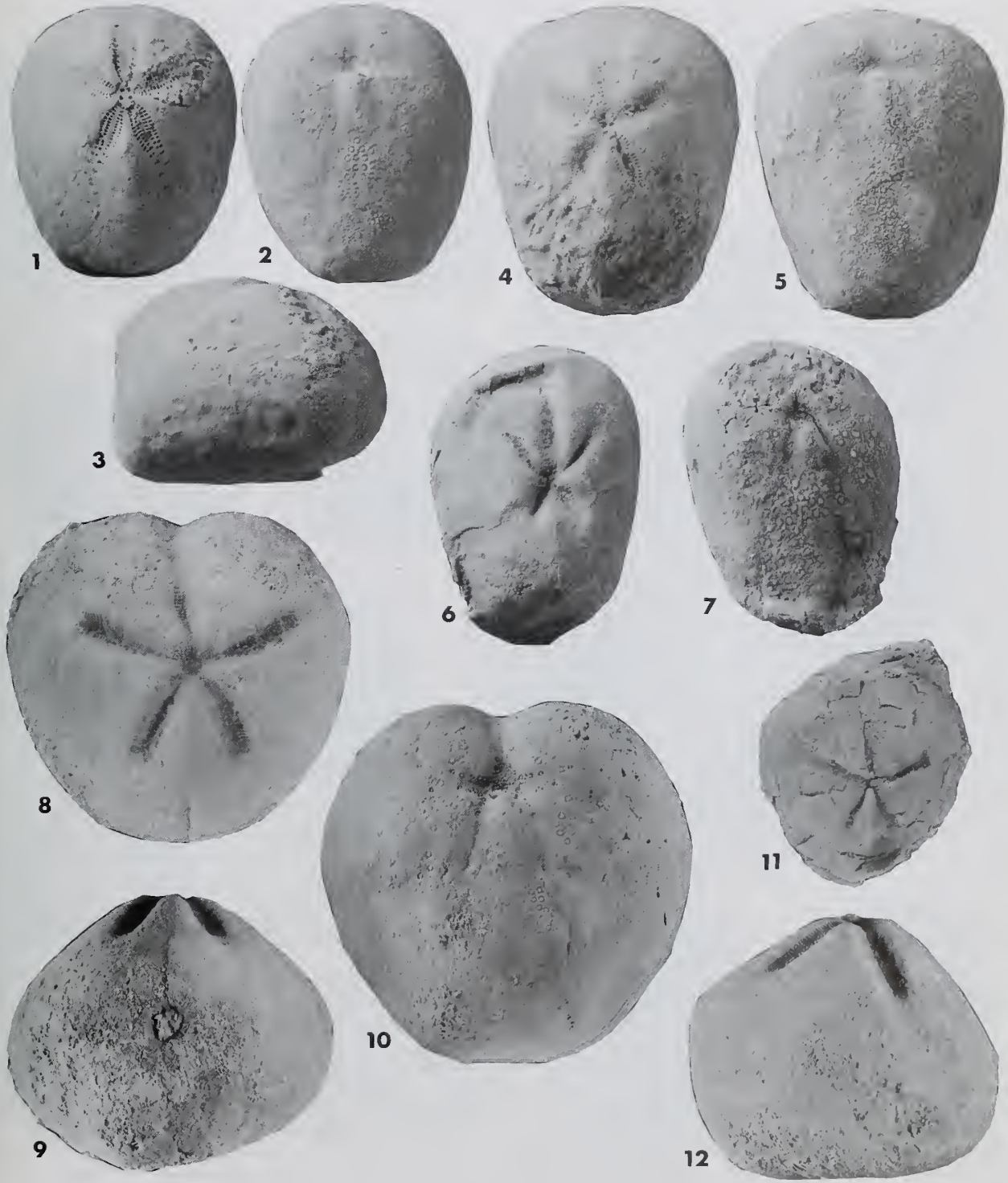
Fig. 30 Camera lucida drawings of plating in *Micraster (Pseudogibbaster) tercensis* Cotteau, 1863, from the late Thanetian of Casas de Oraien (Navarra); **a**, BMNH EE6200, adoral interambulacrum 5, peristome at the top; **b**, BMNH EE4521, apical disc. Scale bars: a = 5 mm; b = 1 mm.

PLATE 8

Figs 1–5 *Cyclaster gindrei* (Seunes, 1888), Danian of Erice, Navarra. **1–3**, BMNH EE6206, apical, oral and lateral views, ×1.5. **4, 5**, BMNH EE6207, apical and oral views, ×2.

Figs 6, 7 *Cyclaster heberti* (Nicklès, 1892), MGB 37551, Maastrichtian of Santander, Cantabria. Apical and oral views, ×2.

Figs 8–12 *Micraster (Pseudogibbaster) tercensis* Cotteau, 1863, Thanetian of Casas de Oraien, Navarra. **8, 9, 12**, BMNH EE4521, apical, posterior and lateral views, ×1. **10**, BMNH EE6200, oral view, ×1. **11**, BMNH EE6201, apical view, ×1.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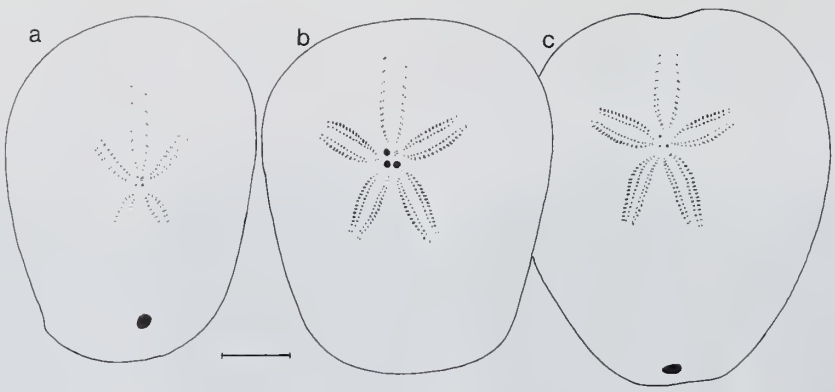

Fig. 31 Camera lucida drawings of plating in *Cyclaster* species. Apical surfaces; **a**, MGB 37551 *C. heberti* (Nicklès, 1892) from the Maastrichtian of the coast west of Cabo Mayor (Santander, Cantabria); **b**, BMNH EE6206 *C. gindrei* (Seunes, 1888) from the Danian of Erice (Navarra); **c**, BMNH EE6208 *C. aturicus* (Seunes, 1888) from the Danian of Erice (Navarra). Scale bar = 5 mm.

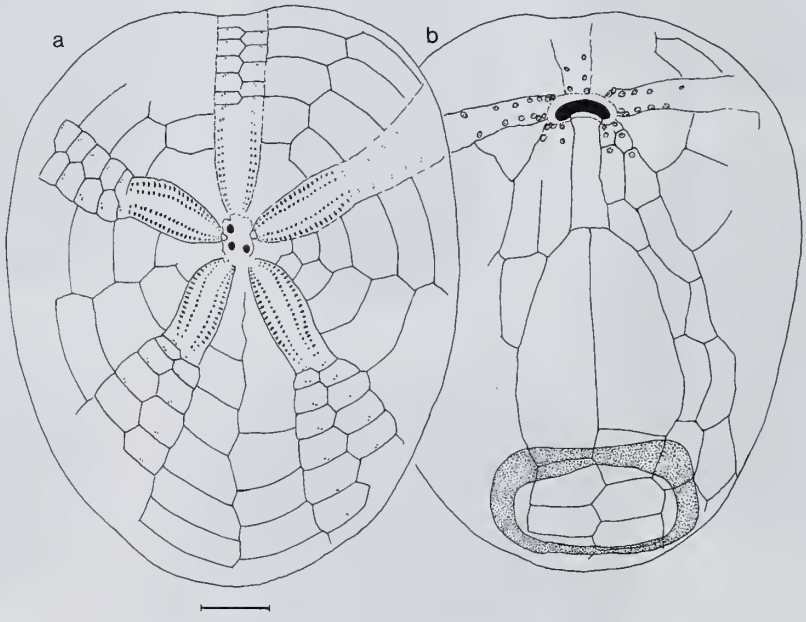

Fig. 32 Camera lucida drawings of plating in *Cyclaster aturicus* (Seunes, 1888) from Astieso hill (Sarasate, Navarra), BMNH EE6068; **a**, apical surface; **b**, oral surface. Scale bar = 5 mm.

PLATE 9

Figs 1–7 *Hemiaster koninckanus* d'Orbigny, 1855, Maastrichtian. **1–4**, BMNH EE6238, Olazagutia Pass, Navarra; apical, oral, posterior and lateral views, ×2. **5–7**, BMNH EE6250, Santander, Cantabria; lateral, posterior and apical views, ×2.

Figs 8–10 *Hemiaster stella* (Morton, 1830), BMNH EE6234, Thanetian of Casas de Oraien, Navarra. Oral, apical and lateral views, ×1.

Figs 11–14 *Hemiaster prunella* (Lamarck, 1816), MGB 37534, Maastrichtian of Santander, Cantabria. Apical, oral, posterior and lateral views, ×2.

Figs 15–17 *Cyclaster aturicus* (Seunes, 1888), BMNH EE6068, Danian of Astieso, Navarra. Oral, apical and lateral views, ×1.

Figs 18–21 *Isaster aquitanicus* (de Grateloup, 1836), BMNH EE6202, Thanetian of Casas de Oraien, Navarra. Posterior, lateral, oral and apical views, ×1.


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OCCURRENCE. Danian of Erice, Navarra Province, Spain; Lower Maastrichtian of Tercis, Landes, France.

MATERIAL STUDIED. BMNH EE6206–07, MGB 37305–06, 37319–21. BMUW 95007, 95008, 95009, 96010, 95011, 95019, 95016.

REMARKS. Differs from the rather similar-shaped *Cyclaster heberti* (Nicklès), from the Maastrichtian of Santander, in having much more widely divergent anterior petals and a less parallel-sided outline. Differs from the contemporary *C. aturicus* in being much less cordiform in outline.

Cyclaster aturicus (Seunes, 1888)

Pl. 9, figs 15–17; Figs 31c, 32

1888a *Isopneustes aturicus* Seunes: 797, pl. 28, fig. 3.

DIAGNOSIS. Test up to 35 mm in length; cordiform in outline with the widest point just behind the anterior petals; tapering posteriorly to a truncated point; rounded anteriorly with a distinct anterior sulcus. Width 85–90% of length. Posterior interambulacrum developed as a keel aborally. Anterior and posterior petals similar in length; anterior pair diverging at about 130°, posterior at about 50°: 18 pore-pairs in petals 6.5 mm in length. Patches of dense granulation at the ends of petals and in the posterior interambulacrum, but no continuous fasciole developed.

OCCURRENCE. Danian, Erice and Astieso, Navarra Province, Spain.

MATERIAL STUDIED. BMNH EE6068, EE6208–6209.

REMARKS. This species has the same petal form as *C. gindrei*, with which it co-occurs, but differs from that species in having a wider, more cordiform test.

Cyclaster heberti (Nicklès, 1892) Pl. 8, figs 6, 7; Fig. 31a

1892 *Isopneustes Heberti* Nicklès: 111, pl. 9, figs 12, 13.
1973 *Isopneustes heberti* Nicklès; Radig: 62, pl. 10, fig. 8, pl. 11, figs 1, 2.
1995 *Isopneustes heberti* Nicklès; Gallemí *et al.*: 269, table 1.

DIAGNOSIS. Test up to 25 mm in length (known to reach up to 45 mm elsewhere). Elongate and subquadrate in outline and with very flattened profile; no posterior keel. Test widest at a point immediately behind where the anterior ambulacra reach the ambitus in plan view; rounded in front without any anteal sulcus. Test tapering slightly to posterior truncation. Anterior petals 30–40% longer than posterior petals; diverging at 90° or slightly less. Posterior petals diverging at 45–50°. No peripetalous fasciole developed, even posteriorly, although traces of granulation may be present around the posterior.

OCCURRENCE. Maastrichtian, horizon 6, of Santander, Cantabria, Spain.

MATERIAL STUDIED. MGB37550–51.

REMARKS. Distinguished from the rather similar-shaped *C. gindrei* by the angle of divergence of its anterior petals, and by its lacking a posterior keel. *C. heberti* was first described from El Matet, Alicante Province, Spain. Topotype material from here reaches 45 mm in length and show variable development of the peripetalous fasciole. Most specimens show traces of the fasciole at the base of the posterior petals while some have more continuous fascioles. A few appear to lack any trace of a peripetalous fasciole whatsoever. Our specimens from Santander show no trace of a peripetalous fasciole.

?*Cyclaster* sp.

OCCURRENCE. Maastrichtian, horizon 4, Olazagutia Pass, and Maastrichtian, black shale facies, Sarasate, Navarra Province, Spain.

MATERIAL STUDIED. BMNH EE6210, EE6211.

REMARKS. The specimen from Olazagutia Pass is a large crushed individual, estimated at 35 mm in length and about 30 mm in width. The apical disc is unfortunately lacking, but the test is cordiform with distinct frontal sulcus and short, well-formed, sunken petals. There is a strong subanal fasciole, but no trace of a peripetalous fasciole. The peristome is non-labiate. The style of aboral tuberculation shows this to be a micrasterid, while the lack of a peripetalous fasciole, relatively short petals and non-labiate peristome suggests *Cyclaster*. However, without better material we cannot be sure about its taxonomic placement. It most closely resembles *C. aturicus* (Seunes) in shape.

The specimen from Irurtzun is badly weathered aborally, but is also rather broad and weakly cordate and is similarly only tentatively assigned to *Cyclaster*.

Genus ***ISASTER*** Desor, 1858

DIAGNOSIS. Ovate micrasterids with weakly conical profile and no frontal sulcus. Apical disc with three gonopores, genital plate 2 lacking a pore. Petals weakly depressed adapically; pore-pairs in all five ambulacra similar. Periproct inframarginal, on inward sloping posterior face. No fascioles.

Isaster aquitanicus (de Grateloup, 1836)

Pl. 9, figs 18–21; Figs 33, 34

1836 *Spatangus aquitanicus* de Grateloup: 176, pl. 2, fig. 17.

DIAGNOSIS. Large tests, up to 65 mm in length, oval in outline and tapering to the posterior. Width 85–95% of length, height 60–70% of length. In profile low domal to subconical with the tallest point coincidental with the apical disc. Apical disc 40–42% test length from anterior; ethmophract. Petals rather short and a little depressed; the two columns being only weakly convergent distally. Anterior paired petals extending only about half the radial distance to the margin, slightly bowed and widely divergent. Posterior petals similar in length to anterior paired petals, but much less divergent. Anterior ambulacrum with enlarged pores in adapical part, which is slightly depressed. This frontal groove is lost towards the ambitus. Peristome kidney-shaped in outline; 20–25% test length from the anterior; downwards facing. Labral plate long and narrow; not projecting over the peristome; sternal plates subequal. Oral surface slightly convex with median part of ridge forming a weak ridge.

OCCURRENCE. Upper Thanetian, *P. pseudomenardii* Zone, Casas de Oraien, Navarra province, Spain.

MATERIAL STUDIED. 71 specimens, including BMNH EE4522–29, EE6069, EE6202–05, MGB 37406–16, 37433–35.

REMARKS. This is the most common species from Casas de Oraien. One-quarter of our specimens have been bored by predatory gastropods.

Family **HEMIASTERIDAE** Clark, 1917

DIAGNOSIS. Spatangoids with peripetalous fasciole, but no subanal fasciole. Dense uniform aboral tuberculation with few intervening granules.

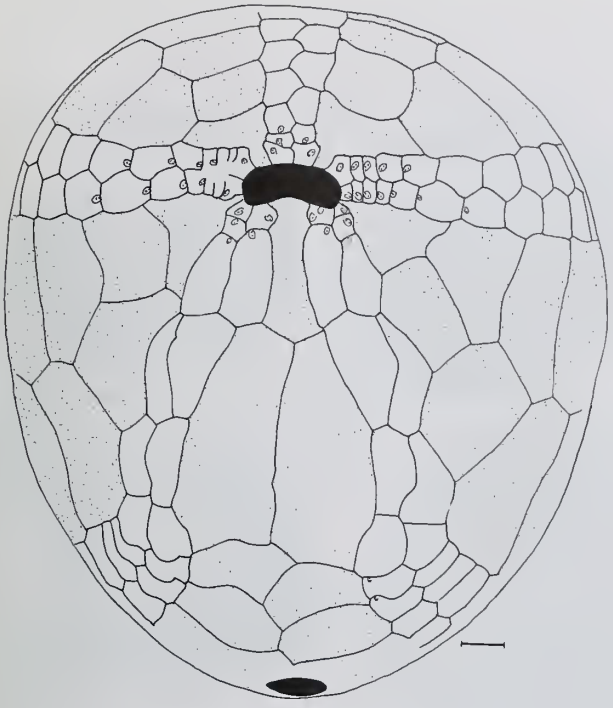


Fig. 33 Camera lucida drawing of plating in *Isaster aquitanicus* (de Grateloup, 1836) from the late Thanetian of Casas de Oraien (Navarra); BMNH EE6202, oral surface. Scale bar = 5 mm.

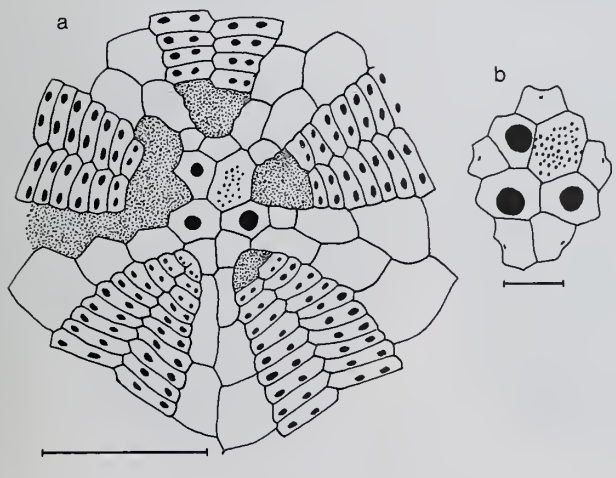


Fig. 34 Camera lucida drawings of plating in *Isaster aquitanicus* (de Grateloup, 1836) from the late Thanetian of Casas de Oraien (Navarra); **a**, BMNH EE6203 apical disc; **b**, BMNH EE6069 apical disc. Scale bars: a = 5 mm; b = 1 mm.

Genus ***HEMIASTER*** Agassiz, *in* Agassiz & Desor, 1847

DIAGNOSIS. Apical disc ethmophract. Anterior sulcus weak or absent.

Hemiaster prunella (Lamarck, 1816)
Pl. 9, figs 11–14; Fig. 35b, c, e

1816 *Spatangus prunella* Lamarck: 33.
1855 *Hemiaster prunella* Lamarck; d'Orbigny: 242, pl. 881.
1856 *Hemiaster prunella* Lamarck; Desor: 122.
1927 *Hemiaster prunella* (Lamarck); Lambert: 50.
1973 *Hemiaster (Bolbaster) batalleri* Lambert; Radig: 61, pl. 10, figs 4–7.
1992 *Hemiaster (Bolbaster)* gr. *prunella* (Lamarck); Gallemí: 347, 350.
1996 *Hemiaster (Bolbaster) prunella* (Lamarck); Wilmsen *et al.*: 354.

DIAGNOSIS. Test up to about 10 mm in length; almost as wide as long; subglobular with weakly domed upper surface; tallest point more or less coincidental with the apical system. In profile, the posterior face is more or less vertical or slopes slightly outwards. Apical disc ethmolytic with four gonopores. Anterior ambulacrum slightly sunken adapically, but becoming flush towards the ambitus; pore-pairs strongly oblique. Anterior petals rather narrow, diverging at *ca.* 110–120°. Posterior petals about half the length of the anterior petals; not strongly bowed. Peripetalous fasciole oval without indentation behind anterior petals. Periproct high on posterior face. Peristome small, kidney-shaped with prominent rim. Labral plate elongate; about half the length of the succeeding sternal plates.

MATERIAL STUDIED. BMNH EE4401–02, EE6240–49, EE6252–61, MGB 37476, 37503, 37515–16, 37518, 37524, 37529, 37534–36, 37538–40, 37547, 37558–59, 37567.

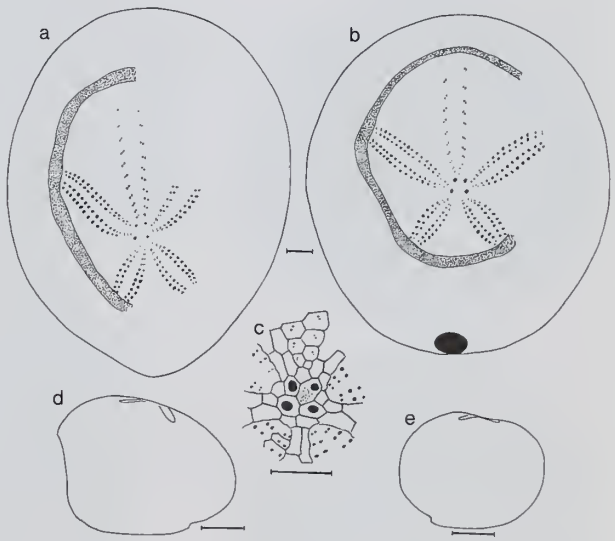


Fig. 35 Camera lucida drawings of plating in *Hemiaster* species. **a**, **d**, *H. koninckanus* d'Orbigny, 1855; **a**, BMNH EE6250, Maastrichtian, coast west of Cabo Mayor (Santander, Cantabria); apical surface; **d**, BMNH 6238, Maastrichtian, Olazagutia Pass; lateral profile; **b**, **c**, **e**, *H. prunella* (Lamarck, 1816); **b**, MGB 37534, apical surface; **c**, BMNH EE6252, apical disc; **e**, BMNH E11093, lateral; b and c from the Maastrichtian of the coast west of Cabo Mayor (Santander, Cantabria); e from the Maastrichtian Maastricht Formation of the Maastricht district, The Netherlands. Scale bars: a–c = 1 mm; d,e = 5 mm.

OCCURRENCE. Maastrichtian, Santander, Cantabria: horizons 2 (21 specimens), 3 (11 specimens), 4 (13 specimens), 5 (13 specimens), 6 (6 specimens). Maastrichtian, horizons 4 and 5, Olazagutia Pass, Navarra. Lower Maastrichtian, Homes Morts Member, Salàs de Pallars and Sapeira, Tremp area (Gallemí, 1992). Elsewhere this species is known from the Upper Gulpen Formation and Lower and Upper Maastricht Formation, Maastrichtian of the Maastricht district, The Netherlands and Belgium (Van der Ham *et al.*, 1987), and the Maastrichtian of the Mons Basin, Belgium (Smiser, 1935).

REMARKS. Many of the specimens are badly deformed and distorted, making certain identification difficult.

Hemiaster koninckanus d'Orbigny, 1855

Pl. 9, figs 1–7; Fig. 35a, d

1855 *Hemiaster koninckanus* d'Orbigny: 250, pl. 885.
1861 *Hemiaster angustipneustes* Cotteau & Triger: 318, 434, pl. 53, figs 5–11.
1984 *Hemiaster koninkanus* d'Orbigny, Van der Ham: 169, fig. 1.
1987 *Hemiaster koninckanus* d'Orbigny, Van der Ham *et al.*: 33, pl. 20, fig. 2.

DIAGNOSIS. Like *H. prunella*, but differing in the following ways: (i) test more elongate, with width 75–85% of test length, rather than almost as wide as long; (ii) in profile, the posterior face is undercut and slopes inwards slightly and the tallest point lies posterior of the apical disc; (iii) the anterior petals are less divergent in smaller individuals, forming an angle of *ca.* 90–100°; (iv) the labral plate projects slightly more over the peristome.

MATERIAL STUDIED. BMNH E6238–39, EE6250–51.

OCCURRENCE. Maastrichtian, Santander: horizon 2 (5 specimens), horizon 6 (1 specimen). Maastrichtian, horizon 2, Olazagutia Pass, Navarra province. Elsewhere the species is recorded from the Upper Gulpen Formation and Lower and Upper Maastricht Formation, Maastrichtian of the Maastricht district, The Netherlands and Belgium.

Hemiaster stella (Morton, 1830)

Pl. 9, figs 8–10

1830 *Spatangus stella* Morton: 245, pl. 3, fig. 11.
1877 *Hemiaster nasutulus* Sorignet; Cotteau: 65, pl. 6, figs 19, 20.
1907 *Hemiaster punctatus* var. *garumnica* Lambert: 720 [*nomen nudum*].
1907 *Hemiaster punctatus* var. *arizensis* Lambert: 721 [*nomen nudum*].
1975 *Hemiaster garumnicus* Plaziat *et al.*: 643, fig. 10.

DIAGNOSIS. Globose test with convex anterior margin; test slightly longer than wide. Apical disc set a little behind mid-length. Anterior ambulacrum with long parallel-sided frontal groove adapically. Anterior petals slightly flexuous, diverging at about 80–90°; shorter than anterior sulcus, but about twice as long as posterior petals. Ovate peripetalous fasciole without indentations.

OCCURRENCE. Upper Thanetian, *P. pseudomenardii* Zone, Casas de Oraien, Navarra province, Spain. Also known from the Thanetian of Landes and the Petites Pyrenées, France (Plaziat *et al.*, 1975).

MATERIAL STUDIED. BMNH EE6237.

REMARKS. Differs from *H. koninckanus* and *H. prunella* in the relative length of the anterior and posterior petals, and in the angle of divergence of the anterior pair, which is much more acute than in either of those species.

Family **CORASTERIDAE** Lambert, *in* Lambert & Thiéry, 1924

DIAGNOSIS. Paired ambulacra non-petaloid to subpetaloid; more or less flush. Apical system ethmophract. Peristome ovate and downward facing; frontal groove feeble to absent. Peripetalous fasciole only.

Genus ***CORASTER*** Cotteau, 1886

DIAGNOSIS. Test globose to ovoid with little or no anterior indentation. Apical disc with four gonopores; test inflated with ambulacral plates relatively tall throughout. Peristome positioned close to the anterior margin and facing forwards.

REMARKS. Distinguished from *Homoeaster* by the much more anterior position of its mouth, and by its proportionally tall ambulacral plates. The peripetalous fasciole of *Coraster* also passes much closer to the apical system posteriorly than is the case in *Homoeaster*. There is considerable variation amongst individuals from the same locality and although many can be placed in one or other of the following species, there is also a good deal of intergradation, making sharp deliniation impossible.

Coraster vilanovae Cotteau, 1886

Pl. 11, figs 4–7; Fig. 37a

1886b *Coraster vilanovae* Cotteau: 70, pl. 9, figs 1–4.
1975 *Coraster vilanovae* Cotteau; Plaziat *et al.*: text-figs 7, 9.
1995 *Coraster vilanovae* Cotteau; Gallemí *et al.*: 269, table 1.

DIAGNOSIS. Test subglobular; almost as wide as tall with virtually no frontal sulcus.

OCCURRENCE. Danian of Erice, Astieso, Larumbe, Navarra. The type locality is the Danian of Les Foies Blanques, Alfas del Pi, Alicante, Spain (Cotteau, 1886b).

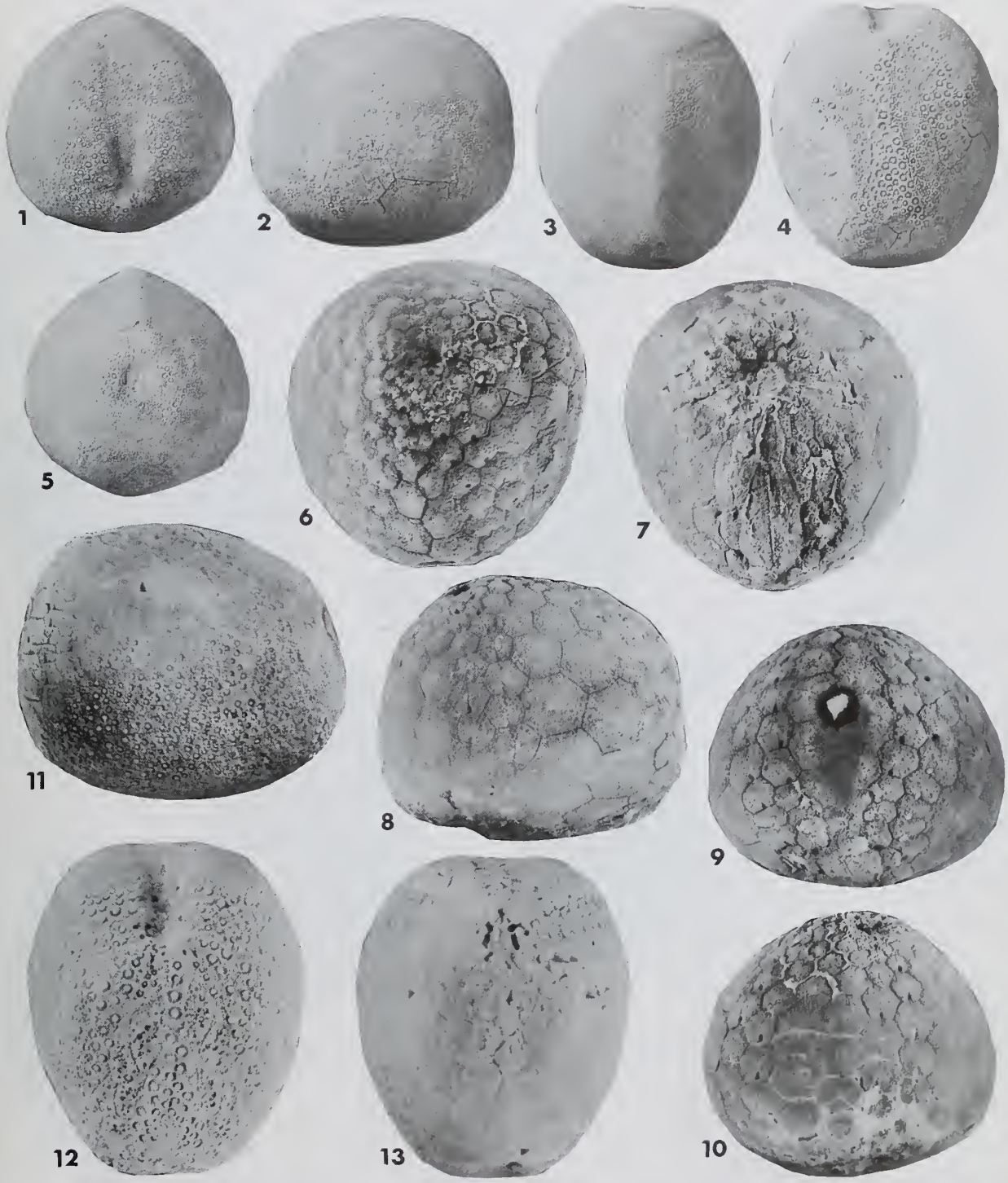
MATERIAL STUDIED. BMNH EE6211–17, EE6226–32, MGB 37307–18, 37325–39, 37365.

PLATE 10

Figs 1–5 *Coraster beneharnicus* Seunes, 1888, BMNH EE4823; Thanetian of Larumbe, Navarra. Anterior, lateral, apical, oral and posterior views, ×1.5.

Figs 6–10 *Ovulaster reticulatus* sp. nov., BMNH EE6074 (**holotype**), Maastrichtian of Sarasate, Navarra. Apical, oral, lateral, posterior and anterior views, ×2.

Figs 11–13 *Coraster beneharnicus* Seunes, 1888, BMNH EE6221; Thanetian of Larumbe, Navarra. Lateral, oral and apical views, ×2.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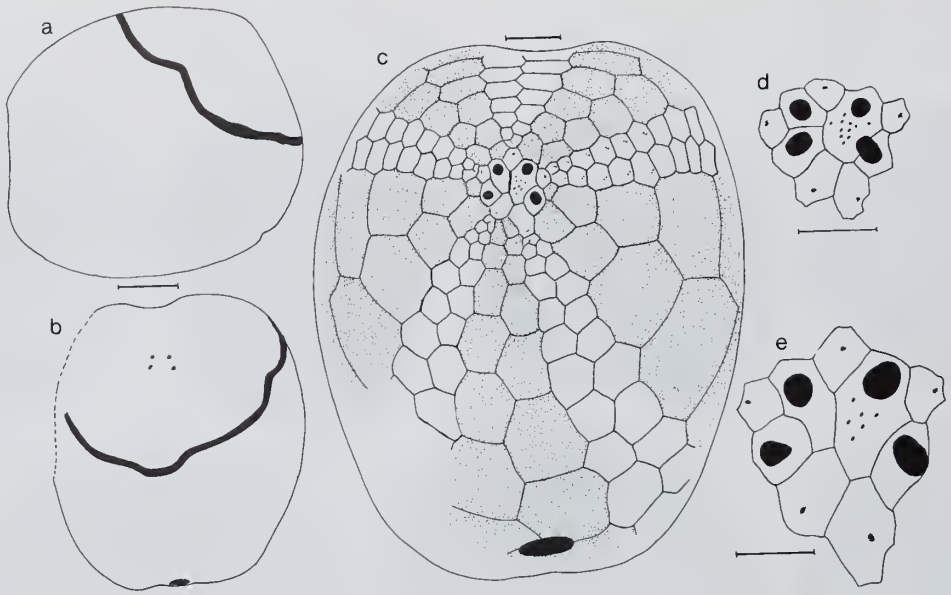

Fig. 36 Camera lucida drawings of plating in *Coraster beneharnicus* Seunes, 1888 from the Danian of Astieso Hill (Sarasate, Navarra); **a**, **b**, BMNH EE6222, **a**, lateral; **b**, apical surface; **c**, **e**, BMNH EE6221, **c**, apical surface; **e**, apical disc; **d**, BMNH EE6223, apical disc. Scale bars: a, b = 5 mm; c = 2 mm; d, e = 1 mm.

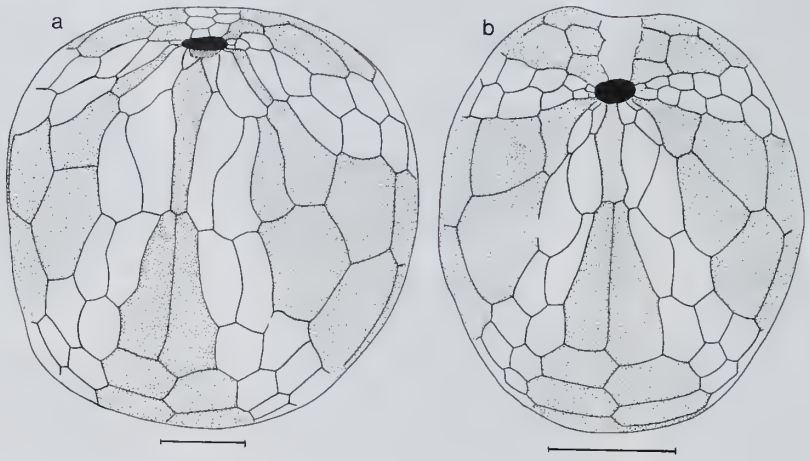

Fig. 37 Camera lucida drawings of plating in *Coraster* species. **a**, *C. vilanovae* Cotteau, 1886; BMNH EE6211 from the early Thanetian of Larumbe (Navarra), oral surface; **b**, *C. beneharnicus* Seunes, 1888; BMNH EE6221 from the Danian of Astieso Hill (Sarasate, Navarra), oral surface. Interambulacra shaded. Scale bars = 5 mm.

PLATE 11

Figs 1–3 *Homoeaster evaristei* (Cotteau, 1886), MGB 37347, Danian of Erice, Navarra. Apical, oral and lateral views, ×2.

Figs 4–7 *Coraster vilanovae* Cotteau, 1886, BMNH EE6212, Danian of Erice, Navarra. Apical, oral, lateral and posterior views, ×3.

Figs 8–12 *Sphenaster larumbensis* sp. nov., BMNH EE6073 (**holotype**), Danian of Larumbe, Navarra. Oral, apical, posterior, anterior and lateral views, ×2.


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REMARKS. The position of the peristome varies from being almost at the anterior margin to around 20% of test length from the anterior.

Coraster beneharnicus Seunes, 1888
Pl. 10, figs 1–5, 11–13; Figs 36, 37b

1888a *Coraster beneharnicus* Seunes: 804, pl. 29, fig. 1.
1975 *Coraster beneharnicus* Seunes; Plaziat *et al.*: 635, pl. 1, figs 1–6, text-figs 6, 8.

DIAGNOSIS. Test slightly longer than wide with weak subanal heel. Anterior ambulacrum forming a broad and shallow frontal groove which deepens adorally and extends to the peristome. Peristome up to 25 % of the distance from the anterior.

OCCURRENCE. Danian of Erice, Astieso, Aristregui, Larumbe, Navarra, Spain.

MATERIAL STUDIED. BMNH EE4822–26, EE4842–44EE6070, EE6218, EE6221–25, EE6233; MGB 37345–46, 37354–62, 37368, 37373–78, 37385–401.

Genus ***HOMOEASTER*** Pomel, 1883

DIAGNOSIS. Test ovate with no frontal groove. Domed to subconical apical surface and flat oral surface. Paired ambulacra non-petaloid to sub-petaloid. Apical system ethmophract and anteriorly positioned, with four gonopores. Peristome small, circular, non-labiate, downward facing. Peripetalous fasciole present, passing just above the periproct posteriorly and at or immediately beneath the ambitus anteriorly.

Homoeaster evaristei (Cotteau, 1886)
Pl. 11, figs 1–3; Fig. 38

1886b *Ornithaster evaristei* Cotteau: 72, pl. 9, figs 5–8.
1892 *Ornithaster evaristei* Cotteau; Nicklés: 115.
1960 *Homoeaster evaristei* (Cotteau); Poslavskaya & Moskvin: 61, fig. 11, pl. 3, fig. 2.
1995 *Ornithaster? evaristei* Cotteau; Gallemí *et al.*: 269, table 1.
1995 *Ornithaster?* sp.; Gallemí *et al.*, table 1.

DIAGNOSIS. Test length up to 30 mm; width approximately 90% of the test length; height 70% of the test length; tallest towards anterior of test. Posterior surface obliquely truncated so that the ovate, longitudinal periproct is just visible from above. Apical system lying 40% of the test length from the anterior margin. Peristome 25% of the test length from the anterior border. Aboral pore-pairs small and slightly circumflexed. Peripetalous fasciole without distinct kink immediately behind the anterio-lateral ambulacra.

OCCURRENCE. Danian of Erice, Navarra. The type comes from the Danian of Alfas del Pi, Alicante province, Spain.

MATERIAL STUDIED. BMNH EE6220, EE6235, MGB 37347.

REMARKS. Distinguished from the closely related Upper Cretaceous *H. tunetanus* by its peripetalous fasciole which follows a weakly undulous path around the test. In *H. tunetanus* the peripetalous fasciole is sharply kinked immediately behind the anterio-lateral ambulacra.

Genus ***OVULASTER*** Cotteau, 1884

DIAGNOSIS. Test highly inflated, with anterior sulcus lacking or extremely feeble. Ovate in profile with posterior tapering to a blunt point. Apical disc ethmophract with four gonopores. Ambulacral plates tall, with small non-petaloid pore-pairs only. Peristome small and circular; slightly depressed. Periproct ovate, placed supra-marginally on steeply sloping posterior part of test. Plastron amphisternous with relatively broad contact between labrum and sternal plates. Subanal fasciole only.

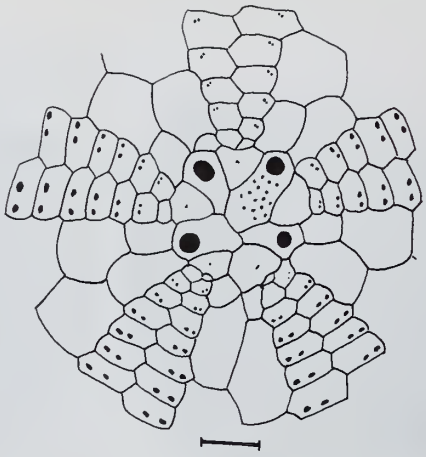

Fig. 38 Camera lucida drawing of plating in *Homoeaster evaristei* (Cotteau, 1886) from the Danian of Erice (Navarra); BMNH EE6220, apical disc. Scale bar = 1 mm.

Ovulaster reticulatus Smith & Gallemí, sp. nov.
Pl. 10, figs 6–10; Figs 39, 40

DIAGNOSIS. Ovate *Ovulaster* with ambulacral and interambulacral plates swollen centrally where they are covered in a coarse reticulate stereom meshwork. Aboral tubercles rather coarse and widely scattered. Lower surface of test flatter than in other species. All ambulacra with reduced and obliquely set pore-pairs. Traces of a subanal fasciole are preserved in the paratype, although much of its tuberculation is missing.

TYPES. Holotype BMNH EE6236, paratype BMNH EE6074.

OCCURRENCE. Lower Maastrichtian black shale facies, Sarasate, Navarra, Spain.

REMARKS. The three previously described species of *Ovulaster* all come from the Coniacian-Santonian of North Africa. Compared to *O. reticulatus, O. zignoanus* (d'Orbigny) is more wedge-shaped in profile and has a slight frontal sulcus. *O. auberti* Gauthier and *O. obtusus* Cotteau are very rounded in profile and lack the flat base seen in our species. All three North African species lack the distinctive tumid plating with its characteristic reticulate stereom meshwork shown by *O. reticulatus*.

Family **SCHIZASTERIDAE** Lambert *in* Doncieux, 1905

Genus ***LINTHIA*** Desor, 1853

DIAGNOSIS. Test cordate with deep anterior sulcus. Paired ambulacra form long, straight, subequal petals. Apical system ethmolytic with four gonopores. Peripetalous fasciole strongly indented between petals. Latero-anal fasciole present. Labral plate relatively short and wide.

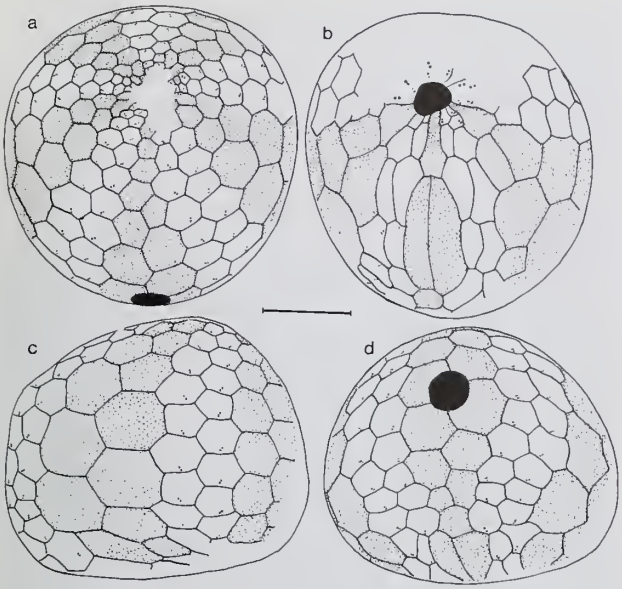

Fig. 39 Camera lucida drawings of plating in *Ovulaster reticulatus* sp. nov. from the Maastrichtian black shale facies at Sarasate (Navarra); holotype BMNH EE6074. **a**, apical surface; **b**, oral surface; **c**, lateral; **d**, posterior. Interambulacra shaded. Scale bar = 5 mm.

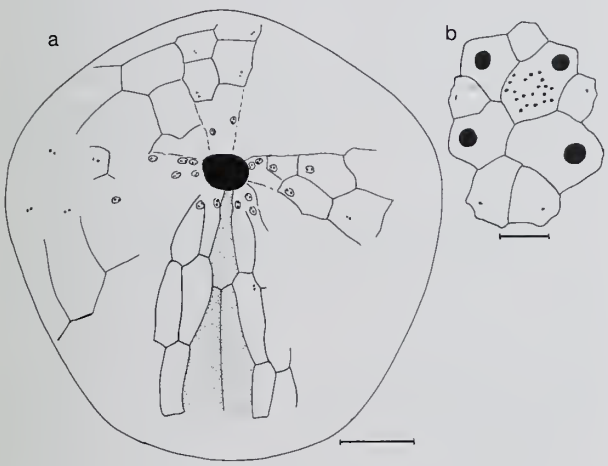

Fig. 40 Camera lucida drawings of plating in *Ovulaster reticulatus* sp. nov. from the Maastrichtian black shale facies at Sarasate, (Navarra); paratype BMNH EE6236. **a**, apical surface; **b**, apical disc. Scale bars: a = 5 mm; b = 1 mm.

?*Linthia* sp. Fig. 41

OCCURRENCE. Upper Thanetian, *P. pseudomenardii* Zone. Casas de Oraien, Navarra Province, Spain.

MATERIAL STUDIED. MGB 37436.

REMARKS. A single specimen showing the characteristic large plastron and very short, wide labral plate of a *Linthia* (Fig. 41). The upper surface is damaged, but shows a rather wide anterior groove and the anterior parts of two sunken petals. Impressions in the infilling sediment suggest that the posterior petals were only about half the length of the anterior pair.

Family **AEROPSIDAE** Lambert, 1896

Genus ***SPHENASTER*** Jeffery, gen. nov.

TYPE SPECIES. *Sphenaster larumbensis* Jeffery, sp. nov.

ETYMOLOGY. From *sphenos* – a wedge.

DIAGNOSIS. Narrow wedge-shaped test. Broad shallowly sunken unpaired ambulacrum with enlarged pore-pairs. Short, flush, non-petaloid paired ambulacra. Ethmophract apical disc with two gonopores. Peripetalous fasciole passes immediately behind the apical system and below the ambitus anteriorly. Enlarged tubercles are developed along the edges of the unpaired ambulacrum.

REMARKS. The new genus is most similar to *Aeropsis*, from which differs in having a wedge-shaped (rather than cylindrical) test with an obliquely truncated posterior, a less anterior apical system and a number of enlarged tubercles on the apical surface. *Aceste* differs in having an ethmolytic apical system, a deeply sunken frontal groove leading to the mouth, single pores in the paired ambulacra and uniform tuberculation. *Sphenaster* is flat across the anterior margin, has pore-pairs in all ambulacra and, although damaged, appears to have no vestibule leading into its mouth.

Sphenaster larumbensis Jeffery, sp. nov.

Pl. 11, figs 8–12; Fig. 42

ETYMOLOGY. Larumbe – the locality at which the specimen was found.

HOLOTYPE. Holotype and only known specimen BMNH EE6073.

OCCURRENCE. Lower Thanetian, upper part of *Coraster* Beds, Larumbe, Navarra Province, Spain.

DESCRIPTION. The holotype measures 14.6 mm in length and 8.4 mm in width (58% of test length). In horizontal outline, the test describes an elongate pentagon. It is flat across the anterior margin, broadens to the widest point (approximately two thirds of test length from the anterior margin) and narrows to the rounded posterior. Maximum height is 10.3 mm (71% of test length), midway along the test. In profile, the test is wedge-shaped, sloping gently to the anterior from the apical system and with a somewhat gibbous lower surface. The posterior is oblique with a very slight subanal heel.

The paired ambulacra are flush and non-petaloid with tiny, inconspicuous pore-pairs. By contrast, the unpaired ambulacrum is broad and slightly sunken and contains enlarged pore-pairs. Pore-pairs are obliquely positioned and diminish in size towards the anterior margin of the test.

The plastron is amphisternous with a long narrow labral plate followed by two equally long, narrow sternal plates. The suture between these plates runs along the midline of the test.

The apical system is positioned 39% of test length from the anterior margin. It has two large genital plates each with a gonopore, and five small ocular plates. A small number of hydropores are present on the madreporite. Plating cannot be clearly made out, but it appears to be ethmophract in structure.

The peristome is circular or rounded pentagonal with no rim. It measures 1.7 mm in diameter (20% of maximum test width) and is situated 21% of test length from the anterior margin. Although the

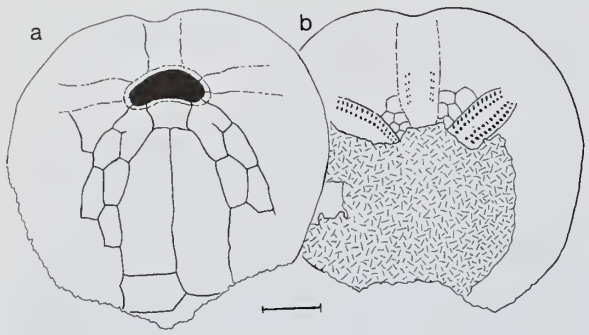

Fig. 41 Camera lucida drawings of plating in *?Linthia* sp. from the late Thanetian of Casas de Oraien (Navarra); MGB 37436, **a**, oral surface; **b**, apical surface. Scale bar = 5 mm.

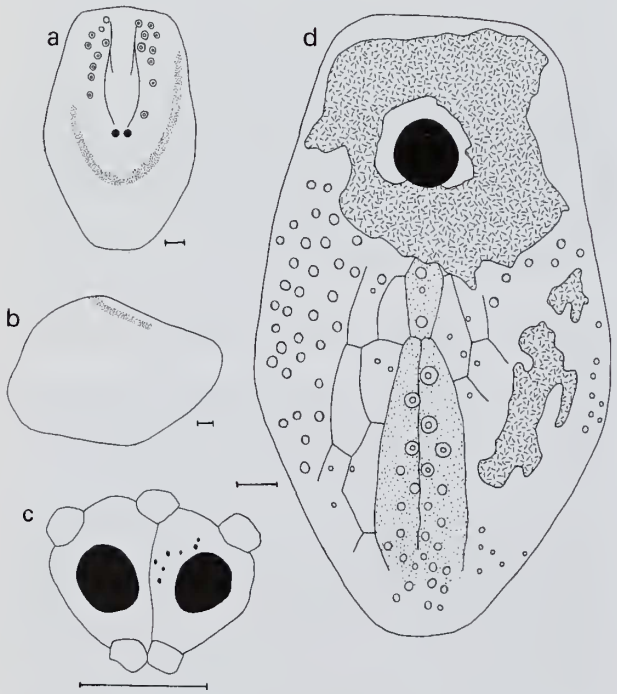

Fig. 42 Camera lucida drawings of plating in *Sphenaster larumbensis* sp. nov., BMNH EE6073 (holotype), from the early Thanetian of Larumbe, Navarra. **a**, apical surface; **b**, lateral profile (fasciole stippled); **c**, apical disc; **d**, oral surface. Scale bars = 1 mm.

oral surface of the test is damaged, it is clear that the labral plate does not extend over the mouth. The periproct is also circular and measures 2.0 mm in diameter. It is positioned high on the oblique posterior of the test, 52% of test height from the base.

A distinct peripetalous fasciole is positioned high on the test. It passes immediately behind the apical system and crosses the anterior margin at the ambitus. At its broadest point, the fasciole is 8 miliaries wide. The fasciole becomes less distinct towards the anterior where a number of small tubercles are incorporated.

Tubercles are perforate and crenulate and are fairly densely distributed over the aboral surface of the test with scattered miliaries in between. The largest tubercles are positioned on the anterior margin at the end of the frontal ambulacrum and on the posterior below the periproct. Tubercles are most densely packed around the periproct. Overall, the test has a somewhat granular appearance. On the oral surface, tubercles are far sparser and on the whole larger than on the upper surface. The largest tubercles are situated on the plastron.

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APPENDIX

Maastrichtian species recorded from the Maastrichtian and Palaeocene of Western Europe (data from Smith & Jeffery, in press)

Species	Distribution		Fate of genus
	Maastrichtian	Paleocene	
Tylocidaris (Sardocidaris) trempina	San, Tre	?Pyrenees	survivor
Tylocidaris (Sardocidaris) ramondi	Nav		
T. (Oedematocidaris) baltica	Dmk, NGer		
T. (Tylocidaris) inexspectata	San, Lim		survivor
T. (Tylocidaris) hemmoorensis	NGer		
Goniocidaris sp. A	Lim		survivor
Phyllacanthus regalis	Lim		survivor
Temnocidaris magnifica	San, Fr		
Temnocidaris danica	Lim	Dmk, Lim	survivor
Temnocidaris nigellensis	Belg Dmk, Eng, NGer	Dmk	
Stereocidaris herthae	Dmk, NGer, Eng, Pol		
Stereocidaris pistillum	NGer, Eng	Dmk	survivor
Stereocidaris sp. A	NGer	Dmk	
Stereocidaris sp. B	Dmk		
Almucidaris falgarsesis	Tre		victim
Cidaris rosenkrantzi	Lim	Lim, Dmk	survivor
Cidaris bolli	Dmk		
Echinothuria sp.	NGer, Lim, Dmk	Dmk	survivor
Centrostephanus sp.	NGer, Lim, Dmk	Lim, Dmk	survivor
Orthopsis miliaris	Lim, Tre, San		
Hyposalenia heliophora	n/p	Lim,Dmk	immigrant
Salenia desori	NGer		
Salenia belgica	Dmk, Belg	Belg, Lim	survivor
Salenia sigillata	Lim, Eng		
Salenia geometrica	Lim, Tre		
Pleurosalenia heberti	Eng		survivor
Pleurosalenia anthophora	NGer, Dmk, Lim, Fr, Belg, Pol		
Pleurosalenia maestrichtensis	Lim, Belg, Nav		
Pleurosalenia pygmaea	NGer, Dmk		
Salenocidaris garumnensis	Pyr		
Salenocidaris gallemi	Alic		
Goniopygus tetraphyma	Pyr, San, Tre		
Goniopygus minor	Lim	Lim, Fr, Belg	survivor
Codiopsis disculus	Tre, Lim	Fr	survivor
Phymosoma hexaporum	Tre, Sant		
Phymosoma granulosum	Dmk, NGer,Belg, San, Fr	Dmk, Lim	survivor
Phymosoma koenigi	NGer		
Diplotagma vanderhami	Lim		victim
Diplotagma sp.	San		
Gauthieria alternans	Dmk, NGer		survivor
'Gauthieria' maeandrinum	Lim		
Gauthieria pseudoradiata	Lim, Dmk, NGer, Belg		
Gauthieria middletoni	Dmk, NGer		
Gauthiosoma princeps	Eng, Dmk, NGer, Lim		
Gauthiosoma krimica	Belg, Dmk	Pol	survivor
Acanthechinus savigni	Pyr		
Acanthechinus sp.	San		survivor
Micropsis batalleri	Tre		survivor
Trochalosoma taeniatum	Dmk, NGer, Lim, Tre, Belg		emigrant
Trochalosoma rutoti	Lim		
Phymotaxis tournoueri	Lim	Pyr	survivor
Circopeltis	n/p	Lim	immigrant
Micropsidia salis	Lim	Lim	survivor
Winkleria maastrichtensis	Lim		victim
Zeuglopleurus werhlii	NGer, Eng		victim
Thylechinus vanderhami	n/p	Lim	immigrant
Coenholectypus nachtigali	Tre, San, Alic		victim
Coenholectypus macrostomus	Lim		
Camerogalerus cantabrius	San		victim
Conulus magnificus	Dmk, NGer		victim
Conulus gigas	Pyr, Tre, San		
Globator darderi	Alic		victim
Adelopneustes boehmi	NGer	Dmk,Lim,Bel	survivor
Galerites vulgaris	Eng, NGer, Alic		victim

APPENDIX Cont.

Maastrichtian species recorded from the Maastrichtian and Palaeocene of Western Europe (data from Smith & Jeffery, in press)

Species	Distribution		Fate of genus
	Maastrichtian	Paleocene	
Galerites stadensis	Dmk, Lim, NGer		
Galerites sulcatoradiatus	Eng, Lim, Dmk, Belg		
Galerites? dollfusi	Rug, Fr		
Echinogalerus belgicus	Lim, Belg		victim
?Echinogalerus vetschauensis	Lim, San		
Echinogalerus muelleri	Lim, San, Nav, Tre		
Echinogalerus? minutus	Lim		
Plagiochasma cruciferum	Lim	Lim, Dmk, Belg	survivor
Catopygus fenestratus	Lim		victim
Hemicara pomeranum	NGer, Pol		victim
Zuffardia sp.	San		emigrant
Faujasia apicalis	Lim		victim
Oolopygus pyriformis	Lim, Alic, San, Fr		survivor
Hardouinia (Fauraster) priscus	Tre		victim
Rhynchopygus marmini	Lim, Fr, ?San		victim
Procassidulus lapiscancri	Lim		survivor
Stygmatopygus bervillei	n/p	Fr	immigrant
Rhyncholampas macari	Lim, San		emigrant
?Gitolampas scrobiculatus	Lim, Sant, Nav		survivor
Neocatopygus arnaudi	n/p	Pyr	immigrant
Nucleopygus coravium	Lim, Belg, San, Nav		emigrant
Nucleopygus carezi	Pyr		
Clypeolampas ovatus	Fr, San, Alic		victim
Oriolampas michelini	n/p	Pyr	immigrant
Galeaster bertrandi	San, Bas	Dmk	survivor
Garumnaster	n/p	Pyr	immigrant
Stegaster altus	Bas, Pyr, Alic, Nav		
Stegaster bouillei	Pyr, Alic, Bas, Nav		
Stegaster cotteaui	Pyr, Bas		
Stegaster heberti	Bas		
Stegaster paleocenicus	Nav		survivor
Tholaster munieri	Bas		victim
Pseudoffaster caucasicus	San, Tre		victim
Echinocorys scutata	Lim, Dmk, Pyr, San, NGer Nav, Alic, Belg, Pol	Alic, Pyr Dmk, Nav	survivor
Offaster pilula	Tre, NGer		victim
Offaster leymeriei	Tre, San, Nav		
Jeronia pyrenaica	n/p	Nav, Pyr,	immigrant
Cardiaster granulosus	Lim, Fr, Tre, NGer, Dmk, Belg		
Cardiaster sp.	Pyr	Nav	survivor
Cardiotaxis heberti	Belg, NGer, Dmk		victim
Hagenowia elongata	Dmk, NGer		victim
Pseudholaster faxensis	n/p	Dmk	immigrant
Hemipneustes striatoradiatus	Lim, Pyr, Nav, Alic		
Hemipneustes pyrenaicus	Pyr, Nav, Tre, San, Alic		victim
Hemipneustes oculatus	Lim		
Hemipneustes sp.	Tre, San		
Micraster schroederi	Lim, Belg, Alic		
Micraster aturicus	Alic		
Micraster grimmensis	NGer	?Dmk	survivor
Mokotibaster nicklesi	n/p	Alic	immigrant
Pseudogibbaster tercensis	n/p	Alic, Nav, Pyr	immigrant
Diplodetus duponti	Lim		
Diplodetus maestrichtensis	Lim		
Diplodetus parvistella	Lim		
Diplodetus coloniae	Alic	Pyr, Belg	survivor
Cyclaster grindrei	San, Pyr	Pyr	survivor
Ovulaster granulosa	Nav		victim?
Cyclaster heberti	Alic		
Cyclaster integer	Pyr	Pyr, Dmk	survivor
Cyclaster platornatus	Rug, Lim		
Cyclaster ruegensis	Rug		
Isaster aquitanicus	Alic	Nav	survivor
Eupatagus mortenseni	n/p	Pyr	immigrant

APPENDIX Cont.

Maastrichtian species recorded from the Maastrichtian and Palaeocene of Western Europe (data from Smith & Jeffery, in press)

Species	Distribution		Fate of genus
	Maastrichtian	Paleocene	
Hemiaster prunella	Fr, Lim, San, Tre, Nav	Dmk	survivor
Hemiaster koninckanus	Lim, San, Nav		
Hemiaster nucula	Fr		
Hemiaster stella	Lim	Dmk, Pyr	
Leymeriaster maestrichtensis	Lim		victim?
Leymeriaster eluvialis	Lim		
Linthia houzeaui	n/p	Belg, Fr	immigrant
Paraster	n/p	Lim, Pyr, Dmk	immigrant
Proraster atavus	Tre	Dmk	survivor
Mauritanaster sp. nov.	n/p	Dmk	immigrant
Coraster vilanovae	Alic	Pyr	survivor
Homoeaster tunetanus	Alic	Alic	survivor
Sphenaster larumbe	n/p	Nav	immigrant

KEY TO LOCALITIES
Alic = Alicante
Bas = Basque region (Zumaia-Bidart)
Belg = Ciply Dmk = Denmark basin
Eng = Norfolk, England
Ger = Pomerania (northern German mainland)
Lim = Limburg (Maastricht region)
Nav = Navarra
n/p = not present
Pol = Poland
Pyr = French Pyrenees (Haute-Garonne)
Rug = Isle of Rügen
San = Santander
Tre = Tremp